COLD WINTERS *VS.* LONG JOURNEYS: ADAPTATIONS OF PRIMARY MOULT AND BODY MASS TO MIGRATION AND WINTERING IN THE GREY PLOVER *PLUVIALIS SQUATAROLA*

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CONTENTS

FOREWORD

This thesis consists of 10 chapters. Eight of these have been published as papers in the scientific literature. The publication details are given on the contents page.

Most of the papers have co-authors. Their contribution to the papers consisted of the provision of bird ringing data and of counts of Grey Plovers at their study sites. All the analyses and the writing of first drafts of papers were undertaken by myself. The co-authors commented on drafts at various stages, and I incorporated their comments into the papers.

SUMMARY

The Grey Plover *Pluvialis squatarola* is a wader (Aves: Charadriiformes) breeding in the high Arctic with one of the widest latitudinal distributions during the boreal winter. Its non-breeding distribution encompasses coastal wetlands from the temperate belt of the northern hemisphere to the southernmost tips of the austral continents.

Following the ecological definition of Alerstam & Hogsted (1982), the Grey Plover is a typical S-species. Its life history is featured by adaptations to ecological restrictions and high intra-specific competition on the breeding grounds: it has a small clutch size, a deferred age of first breeding, an early emigration from the breeding grounds, a post-breeding and post-migration moult ('winter moult'), and a differential migration with adults moving ahead of juveniles. S-species are therefore excellent candidates to study the adaptations of these biological traits, because they have evolved under the effect of intense competition. The Grey Plover, with its cosmopolitan distribution, enhances these opportunities of comparative studies.

Understanding the tight network of ecological, metabolic and energetic relationships between the moult and the other main biological events of the annual cycle (e.g. migration, breeding) is a keystone to unravel the temporal and spatial organisation of migration. Where, when and how long-time migrants moult and build up energy reserves are essential information to understand migration patterns and elucidate the time constraints which act on the migratory system of a species. In this respect, the first information needed to schedule the moult in the context of the other major events are temporal parameters: i.e. the average starting date and the duration of the moult.

A severe limit to the rise of a widespread knowledge of primary moult variation and identification of adaptive patterns was the lack of an efficient statistical method to estimate primary moult parameters. This methodological impasse, originating from an intrinsic weakness of moult field data, was solved by the maximum-likelihood model proposed for avian moult by Underhill & Zucchini (1988) which has been proven to correctly estimate primary moult parameters. However, although the model has been available since 1988, its use has been limited to single populations or sites, apart from one study which has used this model across a wide geographical range, an analysis of the primary moult of the Willow Warbler *Phylloscopus trochilus* (Underhill *et al.* 1992).

The aim of this thesis was to describe the primary moult of Eurasian Grey Plovers spending the non-breeding season at sites widely scattered across the non-breeding range. As in most moult studies, it mainly focused on the moult of primary feathers because this can be considered representative of the whole process under physiological, ecological and evolutionary perspectives. The Underhill & Zucchini model was applied in order to have comparable data. This allowed to investigate the role of distance from breeding grounds and local climatic conditions on moult patterns. The Underhill & Zucchini model was also used, for the first time, to calculate moult parameters of single primaries, offering new insights of the process. Further analyses characterised morphometrically the various populations and the respective age/sex groups, and described the seasonal variation of body mass.

Ringing data originating from seven wintering sites (Great Britain, Italy, Kenya, South Africa, India, NW Australia, SE Australia) were analysed. No field work was organised and carried out *ad hoc* to catch Grey Plovers for this study, except for some trapping sessions in Italy and South Africa; data-sets were gathered from ringing schemes, ringing groups or single ringers who had collected the data over many years of wader ringing. The overall dataset has been collected over the last forty years, from the beginning of pioneer wader ringing to

nowadays. Basic techniques of biometrics and moult data collection were already standardised in the late 1960s and this allowed data to be pooled and compared in various temporal and/or geographical grids.

Morphometric analyses showed that it is not possible in this species to determine the breeding origin of the populations on the basis of some standard measurements and statistical parametric analyses. The application of a recently developed statistical discriminant technique called POSCON (acronym for Posterior probabilitieS and CONfidence intervals; Sluis et al. 1991, Engelmoer & Roselaar 1998) also failed at predicting the breeding origins of birds.

Populations wintering in temperate regions (Britain, northern Italy) had a clear mid-winter peak of body mass, interpreted as an insurance against the effects of severe weather: birds store energy reserves for periods of unpredictable feeding conditions. Southern populations (Kenya, South Africa, India, NW Australia, SE Australia) did not show any seasonal variation of body mass till the respective pre-migratory periods, when energy reserves for a long non-stop flight were stored. Pre-breeding mass increase was temporally segregated from primary moult, while there was a partial overlap of these two metabolic processes during post-breeding migration. Pre-breeding partial moult started only when primary moult was completed and was compatible with mass gain.

The analysis of primary moult of the various populations showed that there were clear differences in moult durations: slow moults (121-131 days) in areas with mild winters and fast moults (90-93 days) in areas with cold winters. Latitude was assumed as an index of weather conditions during the non-breeding period, being negative latitude values of the southern hemisphere linked to the austral summer and positive values of northern hemisphere to the boreal winter. No correlation between latitude and duration of moult was found, while mean starting date of primary moult was correlated to migration distance. This suggested that birds had an optimal moult duration south of 20° N and migrated at about the same speed along the various routes.

Grey Plovers regulated primary moult speed by varying both the number of simultaneously growing feathers and growth rates. Primary growth rate did not change in slow moulting birds, while there was an acceleration throughout the whole moult period in fast moulting birds. This acceleration was interpreted as a response to signals of winter arrival. Feather mass production was not constant throughout the moult period, as it was previously hypothesised, but increased in both groups between P1 and P5. In fast moulting birds mass production increased till P10, while it was constant between P6 and P10 in slow moulting birds, i.e. when 72% of total primary mass is produced. The outermost primary, P10, had a heavier and possibly more resistant structure than the inner primaries, possibly because it forms the leading edge of the wing and must therefore accomplish different aerodynamic functions with respect to other primaries. The hypothesis of structural differences between primaries suggested the existence of species-specific relationships, linked to wing shape and flight characteristics.

A comparison of primary moult durations and primary abrasions suggested that moult duration plays a key-role in determining primary resistance to wear, and hence primary quality. Long moults produce more durable primaries, possibly because they allow the inclusion of higher concentrations of melanins in feather keratins. It is also suggested that primary moult duration and feather quality might contribute to explain why the barycentre of the Grey Plover distribution in the Afro-Palearctic migratory system is around the inter-tropical zone. This would be the closest area to the breeding grounds where birds can find optimal moult conditions.

Data presented in this study suggested that primary moult patterns observed in Europe should be considered as individual adaptations to a new environment rather than a product of genetic evolution because

they seem to be regulated by external factors. The Grey Plover seems therefore a 'tropical' wintering wader which has recently colonised temperate areas.

The thesis consists of ten chapters. The first one is an introductory chapter which presents the state of knowledge on the migration, wintering and moult of the Grey Plover, and addresses a number of questions developed in the following chapters. Chapters 2-8 describe biometrics, moult and migration patterns at a local level (one stop-over site and six wintering areas), while chapters 9-10 investigate and summarise some general patterns and results.

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CHAPTER 1

THE ADAPTATION OF PRIMARY MOULT TO MIGRATION AND WINTERING IN THE GREY PLOVER *PLUVIALIS SQUATAROLA*: A PRELIMINARY OUTLOOK

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The Grey Plover Pluvialis squatarola *is a circumpolar breeding wader with a cosmopolitan winter distribution. Primary moult generally starts only when potential wintering sites are reached. Across the Palearctic-African region Grey Plovers experience an enormous variety of ecological and climatic conditions, which determine the development of different moult patterns, according to local conditions and timing of migration. In the northern part of the winter range primary moult duration was estimated in* c. *90 days, with mean starting and closing dates respectively on mid-August and mid-November. In this area the proportion of birds showing suspended moult during the winter ranged around 20%. In southern Africa, primary moult period was much longer, 130 days, starting on 1 October and finishing on 8 February. No cases of moult suspension were observed. The prolungation of moult period from northern to southern wintering sites has been described for several wader species and it is generally linked with the benign nature of the climate in the wintering area. In Grey Plovers wintering in the Palearctic region, moult duration and closing dates seem to be strictly related to the onset of mid-winter fattening. In absence of a severe winter period, south of* c. *20°N, different populations show a similar moult duration, independently of latitude or distance from the breeding grounds.*

INTRODUCTION

The Grey Plover *Pluvialis squatarola* is a circumpolar breeding wader with one of the widest latitudinal distributions outside the breeding period: it encompasses coastal wetlands from the temperate regions of the northern hemisphere to the southernmost tips of the austral continents (Hayman *et al.* 1986). Because of such a wide non-breeding range, a high diversification of moult patterns among populations can be expected (Kjellen 1994, Marks 1993, Prater 1981).

Moult is a most critical event in the annual cycle of a bird. Moult strategies have proven to be genetically controlled (Berthold 1985, Gwinner & Neusser 1985) and highly adaptive, being regulated by natural selection (Noordhuis 1989, Holmgren & Hedenström 1995); thus, their knowledge at a population level is an important step towards our understanding of the migratory system of a species. In particular, starting date and duration of moult should vary according to timing of migration and environmental conditions at stopover and wintering sites.

The aim of this paper is to describe the moult patterns of Grey Plover at different latitudes and, especially, those of birds wintering at the two ends of Africa, in the Mediterranean and in South Africa. The following questions are addressed: (a) Do moult patterns feature migration routes? (b) Is there a clinal gradient in the duration of moult? (c) Is there an optimal moult duration? (d) Does moult constrain the winter distribution of Grey Plovers?

METHODS

Information on primary moult strategies and parameters (starting and closing dates, duration of moult) have been obtained from different sources along the distributional range. Moult parameters obtained from the literature have been calculated according to different methods, such as eye-fitting, linear regression and maximum likelihood, so that comparisons are not always formally correct and must be considered with caution (cf. Underhill & Zucchini 1988). Nonetheless, it seems that some general trends are clearly visible.

All data refer to the post-breeding moult of birds older than two years. Seasonal terms are referred to their use in the northern hemisphere.

RESULTS AND DISCUSSION

Moult strategies

Grey Plovers, like the vast majority of waders breeding in the high Arctic, start the primary moult after having left their breeding grounds (Cramp & Simmons 1983, Glutz von Blotzheim 1975). Migration and moult are kept temporally segregated, following the general rule that high energetic processes are mutually exclusive and that gaps in the wing area reduce optimal flight performances (Kjellen 1994). Occasionally, some Grey Plovers moult the innermost 1-3 primaries during the incubation period (Cramp & Simmons 1983); recent studies in the Taimyr Peninsula show that probably only males moult on the breeding grounds (Hötker 1995). The presence of a small proportion of migrants with moult suspended at initial stages is also confirmed by observations made at stopover sites visited before the northernmost moulting areas are reached (Gromadzka & Serra 1998).

From available information, two types of migration and moult strategies can generally be described for the Grey Plover. The first is featured by birds which leave the breeding grounds with old primaries (or in suspended moult after having shed the innermost feathers), complete migration, settle at wintering sites and only then begin or resume primary moult. The second case is that of birds which arrest migration at stopover sites located within the winter range of the species, moult a variable number of primaries (till p5-p6, numbered descendently; Boere 1976, Branson & Minton 1976), suspend moult, resume migration and reach their final destination where they complete the moult and spend the winter.

The geographical distribution of these two patterns shows that the first one is the most widespread, featuring populations which winter in the northern Mediterranean, South Africa and India, while the second one is observed only at the northern latitudes of the East Atlantic Flyway and involves those populations which probably do not migrate further south than West Africa (Fig. 1a). In both cases, moult can be suspended if birds face unfavourable winter conditions and then resumed and completed in spring, just before migration. Pre-winter moult suspension seems not to be related to migration routes or to the migration strategy previously adopted (Fig. 1b). The point where moult is eventually suspended in winter is obviously more advanced than that observed during migration, the former usually falling at p7-p9 (Branson & Minton 1976, Serra & Rusticali 1998, van Dijk *et al.* 1986). The proportion of birds which do not complete primary moult by mid-winter is not significantly different (X^2 test) between the Mediterranean (26%, n= 79, data cumulated from Serra & Rusticali 1998 and van Dijk *et al.* 1986) and England (16%, n= 188, Branson & Minton 1976), suggesting the presence of a synchronous timing of migrants arriving at the winter quarters

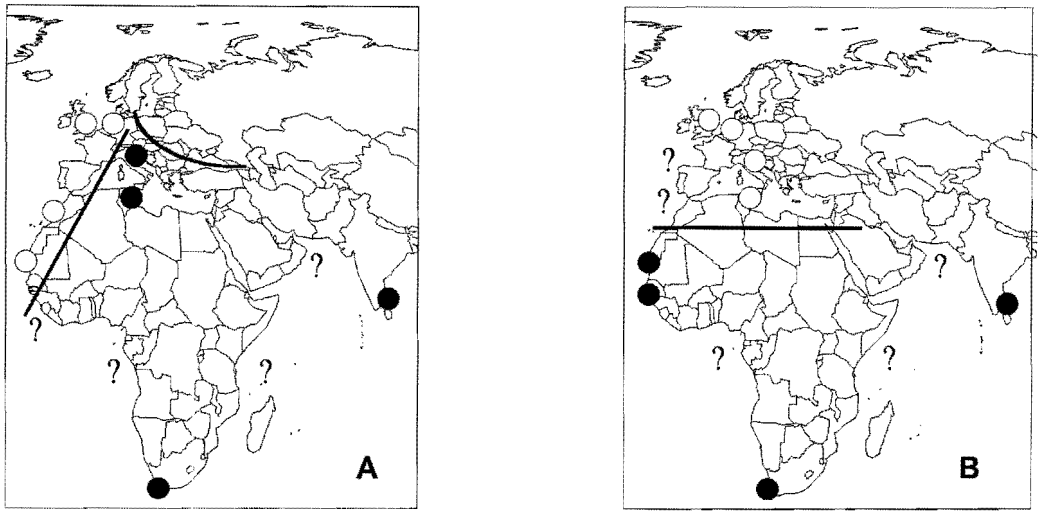

Fig. 1. (A) Geographical distribution of sites where Grey Plovers in suspended primary moult during post-breeding migration are present (empty circles) or absent (filled circles). The straight line divides the East Atlantic Flyway from the esternmost ones. The curved line roughly indicates the northern limit of the winter range. (B) Geographical distribution of sites where pre-winter primary moult suspension is present (empty circles) or absent (filled circles). The straight line, set at c. 20° N, divides the two moult pattern ranges.

Moult timing and duration

Two distinct patterns are apparent also in the estimated moult duration (Table 1): a short moult season (c. 90 days) features populations wintering in northern Europe and in the Mediterranean, while a longer one is required by South-African and Indian Grey Plovers (ca. 130 days).

Mean starting dates of primary moult follow a linear trend with the distance from the breeding grounds (Fig. 2), suggesting that the moult starts immediately after Grey Plovers have reached the wintering areas, and that the delay in the onset of moult is due to the increasing distance. On the other hand, the duration of moult seems not to be linearly correlated to the latitude (Fig. 3). Accepting that latitude roughly reflects winter conditions and day length, two distinct clusters of sites are evident, characterised by favourable and unfavourable winter conditions or long and short daylight periods.

Table 1. Moult parameters of Grey Plovers at different wintering sites.

Site	Duration (days)	Starting date	Closing date	Reference
The Netherlands	90-100	15 August	15 November	Boere 1976
England	90	15 August	15 November	Branson & Minton 1976
NE Italy	93	18 August	19 November	Serra & Rusticali 1998
India	127	1 September	5 January	Balachandran *et al.* 2000
Southern Africa	130	1 October	8 February	Serra *et al.* 1999.

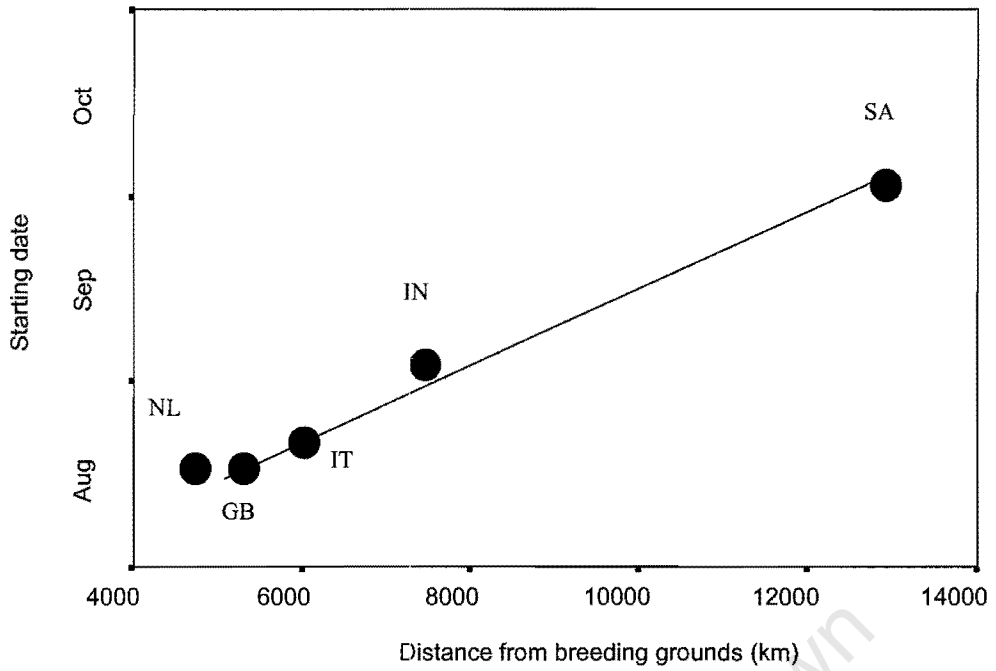

Fig. 2.- Relation between starting dates of primary moult and distances from the breeding grounds. Distances are calculated on the 'great circle' routes from the Taymyr peninsula. IN= India (Balachandran *et al.* in press), IT= Italy (Serra & Rusticali 1998), GB= Great Britain (Branson & Minton 1976), NL= The Netherlands (Boere 1976), SA= South Africa (Serra *et al.* 1999).

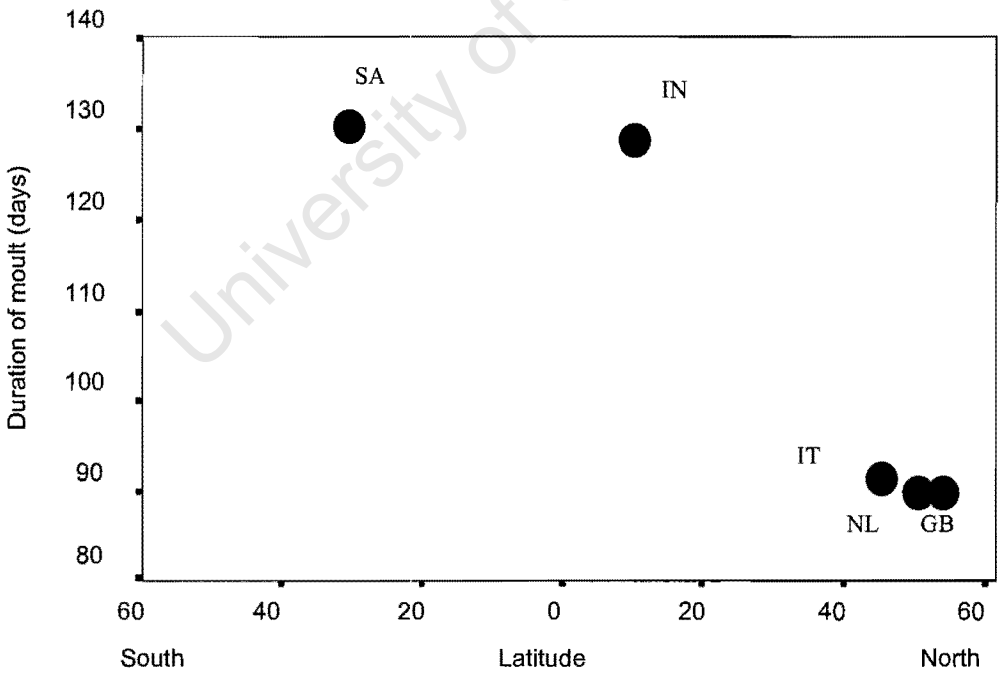

Fig. 3. Primary moult duration of Grey Plovers wintering at different latitudes. IN= India (Balachandran *et al.* in press), IT= Italy (Serra & Rusticali 1998), GB= Great Britain (Branson & Minton 1976), NL= The Netherlands (Boere 1976), SA= South Africa (Serra *et al.* 1999).

The presence of harder wintering conditions at the sites featured by a short moult duration and more favourable conditions where moult proceeds slowly is also shown by body mass values at mid-winter (Table 2). This fits the rule that carrying extra fat loads where (and when) they are not strictly necessary tends to be avoided by wintering birds (Biebach 1996, Pienkowski *et al.* 1984). The lack of a linear trend in the duration of moult is in contrast with the hypothesis that where birds are not forced to close the moult by the arrival of unfavourable environmental conditions, they spread it over as long a period as possible between arrival from and departure to the breeding grounds (Kjellen 1994), in order to minimise energetic demands. This leads to assume the existence of an optimal moult duration for the species, where moult speed can possibly be regulated by the trade-off among the need of maintaining the largest possible wing area, the energetic costs of moult, the trophic features of the wintering (or stopover) sites and, finally, the migratory schedule. Morever, if optimisation leads toward maximising the wing area, in order to enhance flight performances and survival during moult, then the existence of an upper threshold in moult duration, when favourable conditions occur over longer periods, needs to be explained on the basis of ultimate factors possibly connected to a minimum moult speed required by physiological constraints.

Table 2. Mid-winter weights of adult Grey Plovers at different wintering sites.

Site	Mean (g)	S.D.	N	Reference
England	278	-	122	Johnson 1985
NE Italy	250.9	22.9	29	Serra & Rusticali 1998
India	220.1	21.6	207	Balachandran *et al.* 2000
Southern Africa	218.8	16.6	31	Serra *et al.* 1999

CONCLUSIONS

Moult at stopover sites only occurs on the East Atlantic Flyway. A possible explanation is that following these routes, Grey Plovers encounter sites with abundant food resources when they are still at relatively high northern latitudes and attempt to settle for overwintering. Why a proportion of Grey Plovers moulting there should then leave these areas, is still to be investigated. The hypothesis that waders suspend migration and commence primary moult in order to exploit rich food resources *en route* has already been proposed (Pienkowski *et al.* 1976), but does not explain why some Grey Plovers overwinter at sites which others leave. Heavy competition from conspecifics has been suggested as a possible factor for the British estuaries (Townshend *et al.* 1984), but different individual levels of tolerance to severe winter conditions could also be considered. A high degree of facultative adaptability in performing suspended moult strategies is considered likely (Berthold 1996). In particular, tolerance to severe weather might be a sex-dependent character, because males outnumber females in the northern part of the non-breeding range and *vice-versa* (Cramp & Simmons 1983).

The fact that no gradient in moult duration can be detected does not imply its absence. In the Mediterranean and northern Europe, Grey Plovers perform moult at what is probably their maximum possible speed, 90 days, in order to complete it by the incoming winter, and this is confirmed by the presence of pre-winter moult suspension in late birds. South of c. 20° latitude North, Grey Plovers meet more favourable conditions and moult can be performed at what is probably the optimal moult speed for this species, 130 days. Hence, a gradient in moult duration could be observed only at sites where adverse conditions start between 90

and 130 days from bird settlement. In this case, the role of proximate factors in fine-tuning moult duration could be successfully investigated. Along the East Atlantic Flyway, sites where these conditions might be met possibly exist from Iberia to Morocco. Moult data collection in this area might be crucial to improve our understanding of this complex pattern of moult strategies.

At the northern edge of the winter range, Grey Plovers seem to be unable to further adjust primary moult on available time, hence this distribution limit is in agreement with what appears to be the shortest possible moult duration. But, if the southern part of the distribution is considered, moult requirements can eventually explain why Grey Plovers, and waders generally, winter in high numbers in tropical and subtropical wetlands laying around 20° latitude North - these being the closest places to breeding grounds where birds find optimal moult conditions - but they fail to explain why part of the population migrates further south.

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CHAPTER 2

DIFFERENTIAL MIGRATION OF JUVENILE AND ADULT GREY PLOVERS *PLUVIALIS SQUATAROLA* AT THE MOUTH OF THE VISTULA RIVER, POLAND

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Ringing data of 130 juvenile and 65 adult Grey Plovers Pluvialis squatarola *caught between mid-July and mid-October at the mouth of the Vistula River, Poland, in the years 1983-1996 allowed timing and description of a differential migration between these two age classes. Body mass did not vary during the whole period of passage in adults, averaging relatively low values, while an increase in mass towards the end of migration was observed in juveniles. An age-related site exploitation was suggested to explain different daily trapping patterns. Most of the migrating adults had not yet started primary moult, and only 11% were in, or very close to, suspension stages of innermost feathers.*

INTRODUCTION

Adult arctic waders generally leave breeding grounds before juveniles. This behaviour generates patterns of differential migration (*sensu* Gauthreaux 1982, Terril & Able 1988), with adults passing through particular stopover sites earlier than juveniles (e.g. Gromadzka 1987). Differences in timing are associated, at least in some species, with age-specific migration routes, which are usually shorter in adults (Stanley & Minton 1972, Wilson *et al.* 1980). Differential migration has generally been interpreted as an evolutionary product to avoid intra-specific competition at stopover sites, although the role and importance of intra-specific competition on staging migrants has never been ascertained (Berthold 1996).

Along the Atlantic coast of Europe, the autumn passage of adult and juvenile Grey Plovers *Pluvialis squatarola* in two distinct waves is well known. Adults migrate through northern Europe from late July to August, with females preceding males; juveniles appear from late August-September and probably peak in October (Kube & Struwe 1994, Meltofte 1993, Meltofte *et al.* 1994). Nevertheless, detailed information on timing of migration, as well as physiological and moult conditions, was not available for staging sites located north of the main wintering and/or moulting areas. A long-term ringing project carried out in the southern Baltic, just north of the regular winter range, provided data to be analysed to fill this gap.

STUDY AREA AND METHODS

Waders have regularly been ringed and studied at the mouth of the Vistula River (54°21'N, 18°57'E), in northern Poland, since the early 1960s. Ringing seasons generally spanned from mid-July to the end of September. Waders were trapped with walk-in traps, Ottenby type, set along sandy shores facing the sea or the river mouth; the traps were checked daily every two hours, from dawn to dusk (cf. Gromadzka 1981, 1987).

Despite the trapping equipment being specially designed for small *Calidris* species, which were predominant at the mouth of the Vistula River during the study period, larger waders occasionally entered the traps, too.

Grey Plovers do not occur at the mouth of the Vistula in large numbers and usually only single birds or small flocks stop there. Occasionally, flocks of some hundreds have been observed, e.g. mid-October 1978, when about 500 juveniles were found together with about 600 juvenile Dunlins *Calidris alpina*. Data from the period 1983 to 1996 were used in this study.

Grey Plovers were ringed, weighed with Pesola spring balances (accuracy: 2 g), and measured according to standard techniques (cf. Gromadzka & Przystupa 1988). Wing and tarsus plus toe lengths were taken to the nearest mm, total head, bill and tarsus lengths to the nearest 0.1 mm. Primary moult was recorded giving the following scores: 0 = old feather, 1 = feather missing or in pin, 2-4 = progressive stages of growth, 5 = full grown new feather (Ginn & Melville 1983). Birds were aged according to plumage characters (Prater *et al.* 1979).

Where not otherwise stated, data were pooled into 5-day periods (pentades) numbered from the beginning of the year (Berthold 1973), and covering the period 15 July to 14 October (pentades: 40-57). Pentades 40-44 were pooled for body mass analysis, because few birds were trapped so early in the season. Linear regression analyses were performed taking days, numbered from 1 July, as the independent variable. For daily trapping patterns, birds were grouped into eight two-hour classes, from 5h to 21h.

RESULTS

Trapping patterns

Between 1983 and 1996, 130 juveniles and 65 adults were ringed. Only one adult (2%) and eight juveniles (6%) were caught twice at the study area within the same migration season, at one- (5 juveniles and 1 adult), two- (1 juvenile) and three- (2 juveniles) day intervals from capture. The seasonal trapping pattern showed a clear segregation between the passage of adults and juveniles (Fig. 1). The first adults were already on route at the beginning of the study period (mid-July) Their passage showed a bimodal distribution with peaks on 14-18 August (pentade 46) and 29 August - 2 September (pentade 49), followed by a rapid decrease. Juveniles were recorded from late August to mid-October, showing a single peak on 23-27 September (pentade 54).

The daily trapping patterns of juveniles and adults differed significantly (Fig. 2; Kolmogorov-Smirnov test, $z = 1.46$, $p < 0.03$). Adult trapping distribution did not differ from random, maintaining a rather constant trapping rate in the course of the day, while that of juveniles did ($\chi^2 = 31.4$, d.f. = 7, $p < 0.001$). Nevertheless, both age classes showed a maximum just after dawn (5-6 a.m.), followed by a minimum at 7-8 a.m. The number of trapped juveniles then showed a steady increase, reaching a second peak in the early afternoon, followed again by a sharp decline. Subdividing the trapping season into two parts, before 27 and after 28 September (last day of pentade 54 and first day of pentade 55, see next paragraph), the daily patterns of early and late juveniles were not different (Kolmogorov-Smirnov z test).

Biometrics

Wing, total head and bill lengths were significantly different between the two age classes (Table 1). Within each age class, no linear measurements significantly correlated with time expressed by days. The migration season of adults was divided into two periods, up to 23 August (last day of pentade 47) and from 24 August (first day of pentade 48) onwards, to test the presence of biometrically different groups in the two observed migration waves (Fig. 1). Mean wing lengths of the two samples were significantly different (first period: mean = 198.7, S.D. = 3.9, n = 29; second period: mean = 203.1, S.D. = 6.5, n = 20; t-test = 2.92, d.f. = 47, $p < 0.005$).

Table 1. Biometrics of juvenile and adult Grey Plovers ringed at the mouth of the Vistula River in the years 1983 - 1996.

	Age	Mean ± S.D.	Min - Max	n	t	d.f.	p
Wing (mm)	Juv.	196.0 ± 5.7	182 - 224	128	4.7	175	0.001
	Ad.	200.5 ± 5.5	188 - 215	49			
Total head (mm)	Juv.	64.9 ± 2.0	60.0 - 70.0	122	4.3	164	0.001
	Ad.	66.5 ± 2.3	59.5 - 70.0	44			
Bill (mm)	Juv.	28.3 ± 1.2	25.8 - 32.0	127	[1]5.0	95.7	0.001
	Ad.	29.4 ± 1.7	26.0 - 34.0	64			
Tarsus+toe (mm)	Juv.	81.4 ± 3.9	72 - 87	14	1.0	25	0.3
	Ad.	82.8 ± 2.8	76 - 86	13			
Tarsus (mm)	Juv.	47.0 ± 2.0	42.1 - 51.1	34	1.8	59	0.07
	Ad.	48.0 ± 1.9	43.4 - 52.3	27			
Body mass (g)	Juv.	179.0 ± 26.5	112 - 276	129	[1]51.5	181.5	0.12
	Ad.	174.2 ± 15.6	142 - 222	62			

[1] t-test calculated for unequal variance

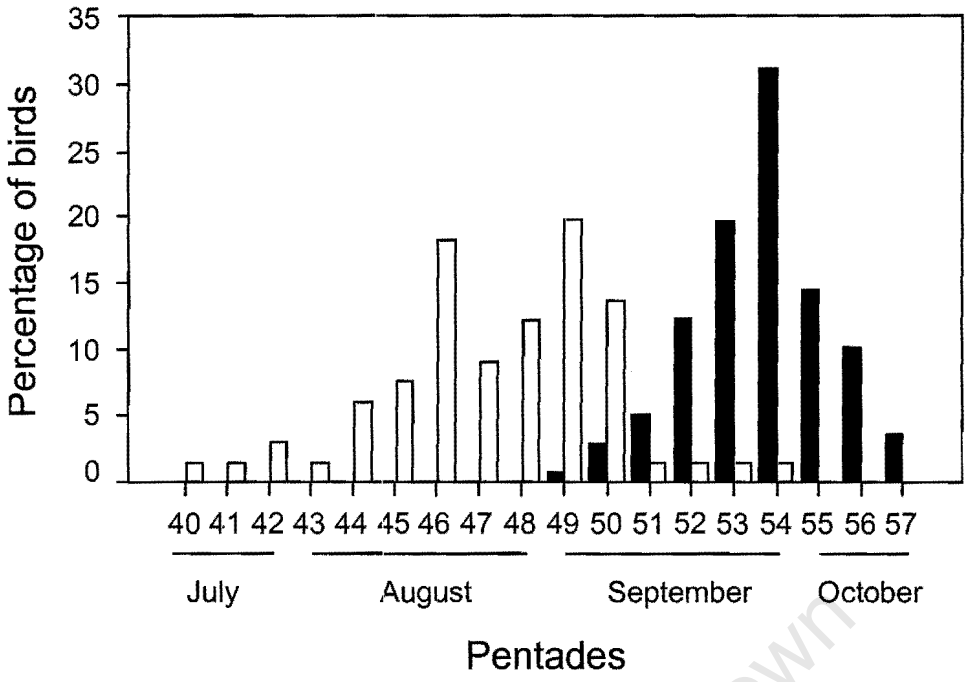

Fig. 1. Seasonal trapping distribution of adult (n = 65; open bars) and juvenile (n = 130; filled bars) Grey Plovers at the mouth of the Vistula River, Poland. Pentade 40 = 15 - 19 July, 57 = 8 - 12 October.

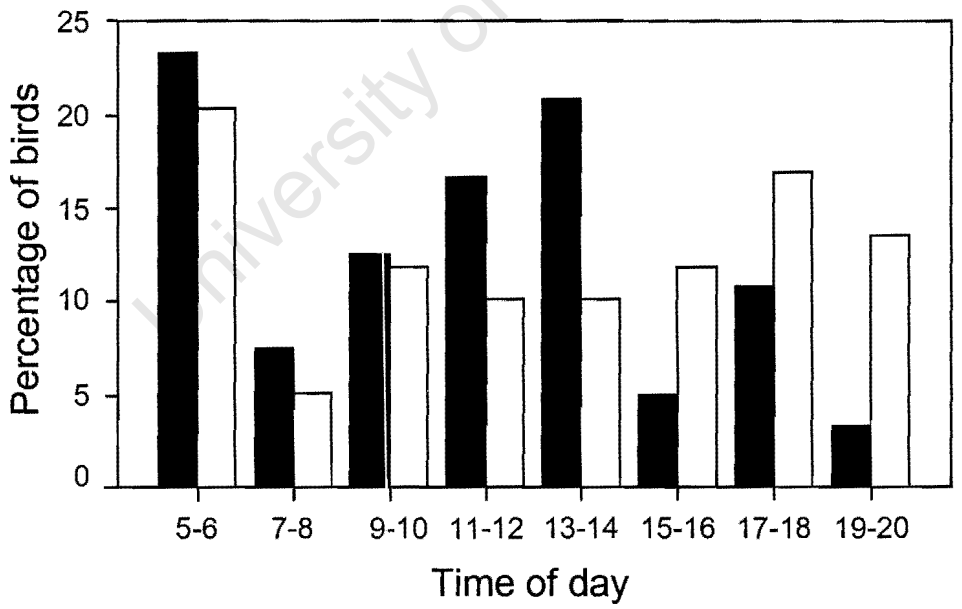

Fig. 2. Daily trapping pattern of adult (n = 65; open bars) and juvenile (n = 130; filled bars) Grey Plovers at the mouth of the Vistula River, Poland.

Adult body mass values did not vary significantly during their period of passage (linear regression of mass on days, F1,61 = 0.76, N.S.), and the same applied to juveniles in the earlier part of their migration period, from 29 August (first day of pentade 49) to 27 September (last day of pentade 54; linear regression of mass on days, F1,88 = 0.36, N.S.) (Fig. 3). Among juveniles, a significant body mass increase was observed regressing mass on days from 23 September (first day of pentade 54) to the end of the season (r2 = 0.43, F1,80 = 59.92, P < 0.0001), when birds averaged about 40 g more than in the first period.

During most of the migration season (up to 27 September, pentade 54) adults were about 6 g heavier than juveniles ($F_{1,151}$ = 4.8514, p < 0.03), averaging 174.2 g (S.D. = 15.6, range 142 - 222, n = 62) and 167.9 g (S.D. = 18.3, range 112 - 222, n = 91) respectively. Later on, from 28 September onwards, after juveniles started gaining mass, they became heavier than adults ($F_{1,98}$ = 61.185, p < 0.001; juv. mean = 205.5 g, S.D. = 24.4, range 163 - 276, n = 38).

Over the whole trapping season, mean body masses did not vary in the course of the day, both in juveniles and adults (one-way ANOVA).

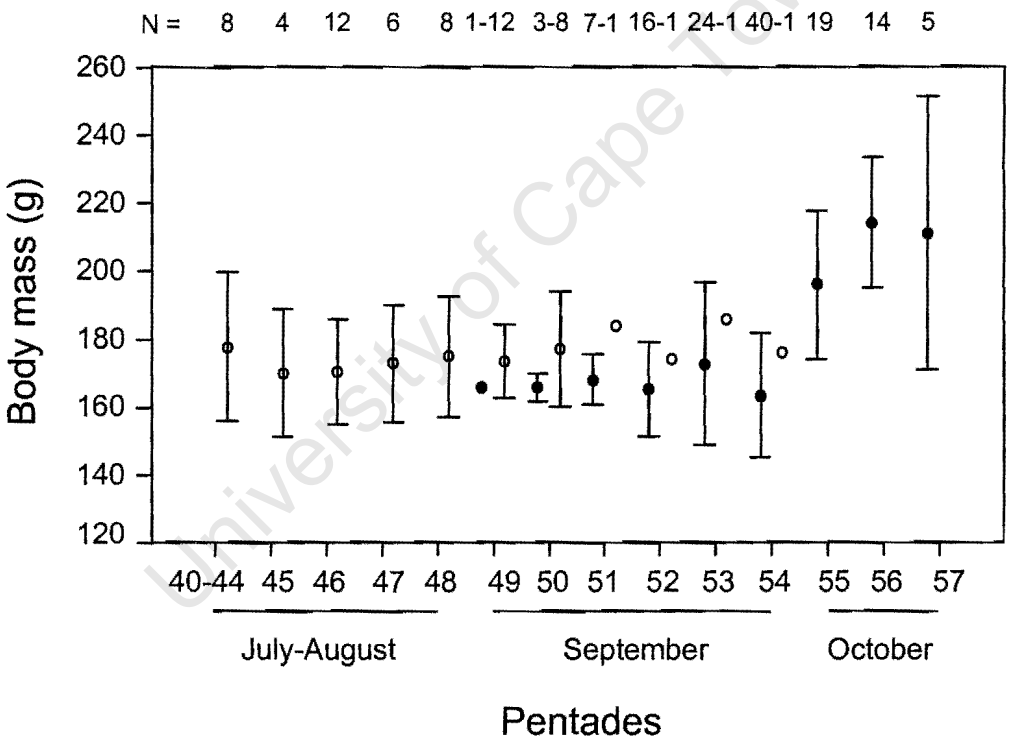

Fig. 3. Seasonal body mass variations of adult (open dots) and juvenile (solid dots) Grey Plovers at the mouth of the Vistula River, Poland. Means, standard deviations and sample sizes are indicated. Pentade 40 = 15 - 19 July, 57 = 8 - 12 October.

Primary moult

All adults (n = 65) were checked for primary moult. Among these, 58 (89%) had not started to moult, five (8%) were in active moult and two (3%) were in suspended moult stages (Table 2). No juveniles showed primary moult.

Table 2. Trapping dates and primary scores (see Methods) of five active and two suspended moulting adult Grey Plovers. Out of 65 adults captured, 58 had not started primary moult.

	Date	Primary score
1	9 August	5440000000
2	14 August	4000000000
3	14 August	5540000000
4	15 August	4400000000
5	25 August	4000000000
6	25 August	5500000000
7	6 September	5550000000

DISCUSSION

A clear pattern of differential migration with a shift in the passage of adults and juveniles was identified, supporting previous information obtained by census data (Meltofte 1993, Kube & Struwe 1994, Meltofte *et al.* 1994).

The daily trapping patterns showed a different use of the area by adults and juveniles. Our data cannot explain whether the hourly trapping rates may be considered an indication of a different feeding behaviour, site prospecting strategy, or simply a differential timing of arrival of newly landed birds, but the existence of age-related migration strategies connected with different site searches, selection and use has been suggested for other waders (Rösner 1990, 1997, Townshend & Evans 1988). In particular, the presence of a peak of activity in the middle of the day could indicate more persistent attempts by juveniles to exploit the feeding resources of the site; adults, conversely, seem to give up sooner and leave. Such a strategy on behalf of juveniles would result in slower rate of migration speed as compared with adults, which is indeed supported by more local retraps.

Adults did not show any seasonal variation in body mass, maintaining relatively low and constant mean values through time (Fig. 3). With respect to Grey Plovers staging at the Wash, England, in August, in Morocco in September, and at the Banc d'Arguin, Mauritania, in October, Polish birds were, respectively, 23%, 12% and 18% lighter (Dick & Pienkowski 1979, Johnson 1985, Lesink & Meininger 1990). Hence, if an increase in pre-migratory body mass on the breeding grounds or in their close proximity is assumed - for which no information is available - this result would suggest that adults stopping at the mouth of Vistula River are newly landed birds, perhaps at their first stopover from the breeding grounds, after a long non-stop flight. On the other hand, a route covered with short flights and frequent stopovers, which would, theoretically, imply carrying low energy loads under an optimal migration perspective (Alerstam & Lindström 1990), can probably

be excluded considering how the species behaves in other parts of the east Atlantic flyway (Branson & Minton 1976, Summers & Waltner 1979, Zwarts *et al.* 1990).

The juvenile seasonal body mass pattern resembled that of adults for most of the migration season, but showed a sudden change during the final period (October) when juveniles carrying large energy reserves appeared (Fig. 3). Towards the end of the passage, the need for storing energy for a further migration step - because of its endogenous control (Berthold 1975, 1984) - could be strong enough to force birds to start mass gain independently of latitude and/or trophic quality of the site they have reached. This fact should be reflected in longer stays and, probably, different daily rhythms of activity. However, our data failed to show such hourly differences between early and late migrants, probably because no really suitable spots to replenish energy reserves were available and, consequently, juveniles did not stay long after they had tested the quality of the site.

The onset of primary moult on the breeding grounds (Cramp & Simmons 1983, Hötker 1995) and the arrival at the main moulting areas of birds showing the innermost 1-3 primaries in suspended moult stages were already known (Boere 1976, Branson & Minton 1976). Five out of 10 males (50%) and 1 out of 14 females (7%) ringed on the Taimyr Peninsula between 28 June and 20 July 1989-91 were in active primary moult (Hötker 1995). Similarly, at Sibiryakov Island (72°44N, 79°08E) in summer 1990 and at the mouth of the Pyasina River (Taimyr, 74°07N, 86°52E) in 1991, five males (19%) out of 26 trapped, whereas none of the 29 females, were moulting at the same time (P. Chylarecki & A. Sikora pers. comm.). On the Yamal Peninsula, none of the 90 breeders caught between 21 June and 20 July in 1990-1995 was in active moult, possibly because most birds were ringed around the end of June and the beginning of July (V. Ryabitsev pers. comm.). On Taimyr, for birds selected after 14 July, when the first moulters were found, the proportions of moulting birds in the two samples were 38% (n = 18) and 27% (n = 19), respectively. Furthermore, these data suggest that the majority of Grey Plovers found in suspended or active moult during the first part of the post-breeding migration are males.

Frequencies of birds in suspended or active moult at the mouth of the Vistula River (11%) were lower than those observed in Taimyr or at the Wash. Different moult strategies at a population level can hardly be considered to explain this pattern, as the onset of primary moult in males seems a widespread phenomenon throughout the breeding range. An alternative hypothesis might involve differential migration between sexes, with more females stopping-over at the mouth of the Vistula River than elsewhere in western Europe. In the western Palearctic, females might follow more eastern routes than males, heading directly to wintering areas of tropical and subtropical Africa where they outnumber males (Cramp & Simmons 1983). The presence of longer-winged birds in the second wave of adult passage and the almost complete absence of birds in primary moult among late migrants suggest that these birds are probably mostly females originating from a different population.

Despite our data showing that some birds migrate in active primary moult, only moult stages close to suspension were actually observed, suggesting that primaries were shed before the beginning of the journey and apparently confirming that, like most waders migrating with long non-stop flights, Grey Plovers tend to maintain a temporal segregation between migration and moult.

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CHAPTER 3

BIOMETRICS AND MOULT OF GREY PLOVER *PLUVIALIS SQUATAROLA* IN NORTHEASTERN ITALY

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Grey Plovers Pluvialis squatarola *wintering in northeastern Italy were morphometrically closer to the populations which use the East Atlantic Flyway than those following eastern routes, but differences in biometrics appeared too small for reliable considerations on breeding origins. Body mass seasonal variations showed a clear mid-winter peak, reaching 250 g both in adults and first-years. No body mass increase was observed in spring, suggesting early, short movements to pre-migratory staging areas where energy reserves are accumulated. Adult primary moult was estimated in 93 days, with mean starting day on 18 August and mean closing date on 19 November. Two concurrently active primary moult cycles were observed on second year birds in September-October.*

INTRODUCTION

The Grey Plover *Pluvialis squatarola* is a circumpolar, monospecific breeding wader with a slight clinal morphometric variation in wing length and bill shape along its Palearctic breeding range (Glutz von Blotzheim *et al.* 1975, Cramp & Simmons 1983). Western Siberian birds, breeding eastward to Taimyr Peninsula are characterised by short wings and bills, migrate along the East Atlantic Flyway and winter southward to West Africa (Branson & Minton 1976, Prokosch 1988, Smit & Piersma 1989, Wymenga *et al.* 1990, Exo & Wahls 1996). Eastern Siberian birds are larger and are supposed to follow more direct, inland routes to the Mediterranean-Black-Sea region (van Dijk *et al.* 1986, Spiekman *et al.* 1993), reaching also the western shores of Africa till its southern tip (Summers & Waltner 1979, Harrison *et al.* 1997).

The Mediterranean wintering population was estimated in 26 000 birds, compared with 168 000 calculated for the whole East Atlantic Flyway inclusive of the Mediterranean (Smit & Piersma 1989). Grey Plovers are mainly concentrated in Tunisia and Italy, smaller numbers being present in Egypt, Spain and France (Smit 1986, Velasco & Alberto 1993, Atta *et al.* 1994, Baccetti *et al.* 1996). Large flocks seem to occur only in the tidal areas of the Gulf of Gabès, Tunisia, and in northeastern Italy. These two areas supporte over 50% of the total Mediterranean wintering population (van Dijk *et al.* 1986, Baccetti *et al.* 1996).

Despite its relatively broad distribution and almost continuous seasonal presence in the Mediterranean coastal wetlands, very little is known for this region about phenology (Motis *et al.* 1981, Martinez Vilalta 1985, Britton & Johnson 1987, Casini *et al.* 1992), biometrics and moult (van Dijk *et al.* 1986, Spiekman *et al.* 1993, Meininger 1994). Available information on measurements and moult for the Palearctic breeding populations comes from northwestern Europe (Meise 1952, Boere 1976, Branson & Minton 1976, Prokosch 1988), west Africa (Pienkowski *et al.* 1976, Dick & Pienkowski 1979, Ens *et al.* 1989, Lesink & Meininger 1990, Wymenga *et al.* 1990, 1992) and India (Balacandran *et al.* 2000).

The aims of this paper are to describe biometrics of the northeastern Italian wintering population and to discuss, within the framework of what is known about Palearctic populations: (a) the primary moult pattern of adults and second-year birds; (b) the seasonal body mass variation in relation with bird age and timing of migration.

STUDY AREA AND METHODS

Grey Plovers were captured at two of the most important wintering sites in Italy: the Lagoon of Venice (45°11'-45°33'N, 12°07'-12°38'E) and the Po Delta (44°48'-45°11'N, 12°15'-12°32'E). These two areas stretch for *c.* 140 km along the north Adriatic sea coast, forming an almost continuous chain of wetlands. A wide variety of habitats are present, from fresh- to hypersaline-waters. Grey Plovers were usually observed feeding on tidal mudflats and roosting on sandy beaches or sandbars. In the Lagoon of Venice the pans of traditional fishfarms ('valli') were also used when pans were dry or water levels lowered, according to fish production seasonal requirements. The median mid-January population size for the Lagoon of Venice between 1992-96 was 256, while in the Po Delta 335 birds were counted in January 1994 (Baccetti *et al.* 1996). The Italian grand total was estimated at *c.* 1750 wintering birds, 51% of which was concentrated in the Lagoon of Grado and Marano, bordering the northern edge of the study area (Baccetti *et al.* 1996).

Grey Plovers were trapped at night in mist-nets at high tide roosts or during pre-roosting movements between 1990-96 in the Lagoon of Venice and 1988-96 in the Po Delta during regular year-round wader ringing activities carried out 1-2 times per month, according to spring tides and weather conditions.

The non-breeding period from August to May is hereafter referred to wintering season. The year was divided into days, numbered from 1 July.

Birds were aged according to Prater *et al.* (1977) and Cramp & Simmons (1983), mainly relying on features of upper wing coverts for the identification of first-year birds and on primary abrasion and moult pattern for separating second-year from older birds. Some second-years still retained some upper wing inner median coverts of the juvenile plumage by October, after the end of their first complete moult. The following age categories have been used: first-year (1y) = bird in its first year of life from 1 July to 30 June; second-year (2y) = bird in its second year of life from 1 July to September/October; third-year or older (3y+) = bird after its second year from 1 July until the end of primary moult in September/November; adult = bird after its first year from 1 July to 30 June: second-years, when identified, have not been included among adults. Apart from primary moult and wing length analyses, birds were usually divided into first-years and adults.

All birds were ringed and the following standard measurements were taken according to Prater *et al.* (1977): maximum wing chord and tarsus+toe lengths to the nearest mm by means of a stopped ruler, total head, bill from feathering, nalospi (distance from the distal edge of the nostril to bill tip) and tarsus lengths to the nearest 0.1 mm with a dial calliper. Body mass was recorded with electronic balances with a digital scale of 0.1 g. Birds were usually processed within 1 hour from net-checking and no correction was applied for body mass decrease. First-years retrapped in wintering seasons following that of ringing have been considered for their first retrap (no second retraps of the same first-year have occurred) as new birds and included in all the adult analyses, while adult retraps have been excluded from all the analyses except for temporal presence. It has been assumed that after 30 November all first-years had completed wing feather and body growth, and in order to test this hypothesis they have been divided in two groups: birds caught before or after this date.

Primary moult was recorded according to Ginn & Melville (1983), scoring old feathers 0, new ones 5 and growing ones 1 - 4. Primary moult scores were then converted to percentage feather mass grown (PFMG) using relative masses calculated by Underhill & Summers (1993). Timing, duration and speed of moult were obtained applying the model of Underhill & Zucchini (1988) and we considered the data to be of type 2: i.e. it has been assumed that the population arrived in the study area before the onset of moult and remained in the area thereafter. Birds in suspended primary moult or with two active moult centres were excluded from the calculation of the moult parameters.

The seasonal variation of body mass was described using the weighed moving average of Summers *et al.* (1992), applying a stronger smoothing parameter, 20 instead of 10 in equation 1 of the above mentioned paper, accounting for the smaller numbers of observations available in our sample (cf. Balachandran *et al.* in press).

RESULTS

Ringing results and recoveries

In seven consecutive years of activity, 114 adults (August-May), 16 second-years (July-October) and 65 first-years (September-May) have been ringed; no recoveries of foreign ringed birds were made or recoveries of our birds abroad have been reported by now. So far, only one recovery links Italy with other countries: one bird ringed at Langebaan Lagoon (33°12'S, 18°07'E), South Africa, on 7 February 1981, was collected at Savio river mouth (44°18'N, 12°18'E), 75 km south of Po Delta, on 20 August 1985 (ring PRETORIA D 6020).

Nineteen local recoveries (15 ringing retraps and 4 shot birds) were obtained from the Po Delta out of 111 adults and 61 first-years ringed there, all coming from areas neighbouring the ringing site. Four adults were retrapped within the same wintering season, after 10, 29, 162 and 182 days respectively (dates: 13/10 - 23/10/1990; 20/1 - 18/2/1993; 21/9/1991 - 2/3/1992; 9/9/1991 - 10/3/1992). Fifteen birds (12 adults and three first-years) were recovered in following wintering seasons, nine after one and six after two. The overall period of presence spans between early September to mid-March (Fig. 1).

Biometrics and body mass

Wing length difference between 3y+ birds with old primaries (August-November, $\bar{x}$ = 202.9 mm, S.D. = 4.3, n = 24) and adults with a new set (October-December, $\bar{x}$ = 206.2 mm, S.D. = 3.3, n = 17) was significant (t-test = 2.62, p = 0.012), accounting for 3.3 mm, i.e. 1.6% of total length. Nevertheless, a linear regression of adult wing length on days between October and May was not significant (r = 0.23, $F_{1,45}$ = 2.63, p = 0.11). Consequently, wing length for the local wintering population was estimated grouping all the adults caught in October-May, considering only the birds which attained a complete moult. The existence of a similar relation with time was assumed also for tail length.

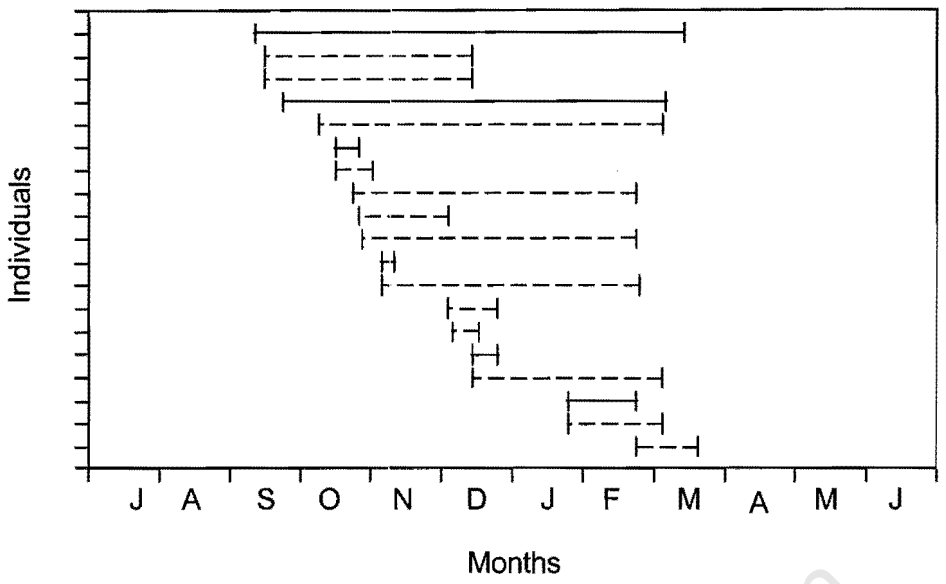

Fig. 1. Elapsed time between ringing and recovery of 19 Grey Plovers in northeastern Italy. Solid lines indicate that ringing and recovery have occurred in the same wintering season, dashed lines represent recoveries obtained in following years, i.e. dates have been connected ignoring possible differences in timing of presence in the area between years.

First-years were significantly smaller than adults in all measurements but tarsus+toe (Table 1). First-years averaged *c.* 4-5% less than adults in bill and nalospi length, *c.* 3% in wing length, and *c.* 2% in total head and tarsus length.

Linear regressions of all the first-year measurements as dependent variables on time period reported in days from 1 July were not significant. Dividing the first years into two temporal classes (Table 2), before and after 30 November, significant differences were observed between each of the two first-year classes and adults for wing and tail lengths, while no differences were found between first-year categories (Table 3). Total head and nalospi lengths of the earliest group of first-years differed by the second one and adults, while bill lengths were different between each age/time category; tarsus lengths differed only between the earliest group of first-years and adults (Table 3).

Both age classes built up weight in November, showing a broad winter plateau spanning from December to February and a following, rapid decrease in March (Fig. 2). Between September and November, when both age classes were present, first-years were leaner than adults, although means were significantly different only in October (t-test; $t=3.90$, $df= 47$, $p< 0.001$), probably due to the low numbers of birds sampled in the other months (Table 4). From the onset of winter to spring, monthly means of first-years and adults varied according to the same pattern and showed very close mean and range values. No birds were available for June and only a few for April and May (Table 4). There is no evidence of pre-migratory spring body mass increase, but the lowest values observed in May among adults might be referred to passage birds.

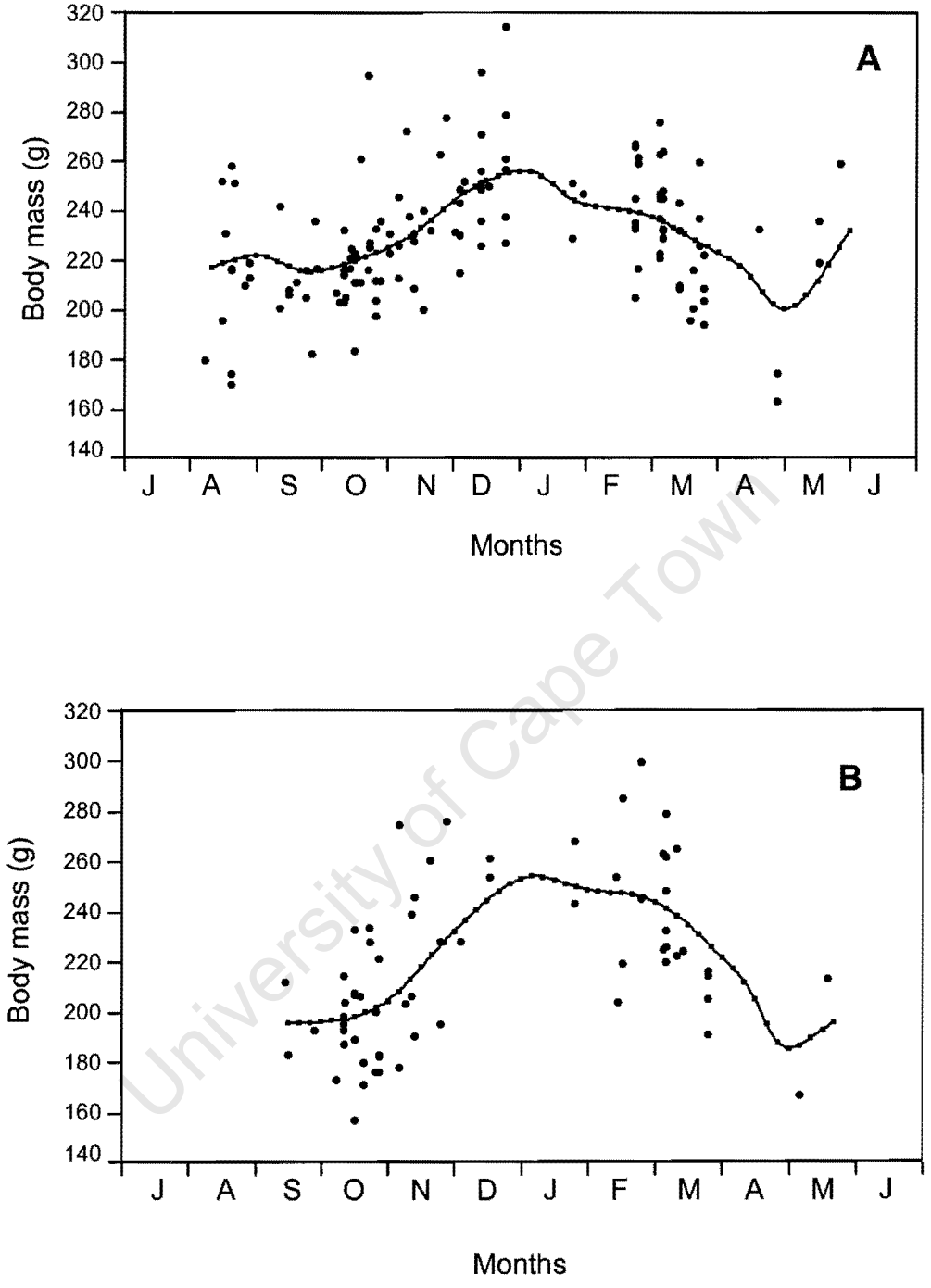

Fig. 2. Temporal variation of body mass in first-year (a) and adult (b) Grey Plovers in northeastern Italy. Lines represent smoothed means (see Methods). Dots refer to one or more birds.

Table 1. Biometrics of first-year and adult Grey Plovers ringed in northeastern Italy between 1988-96 and t-tests between the measurements of the two age categories.

	First-years			Adults					
	Mean ± S.D.	Min-Max	n	Mean ± S.D.	Min-Max	n	t	df	p
Wing[1] (mm)	197.8 ± 6.1	182-212	63	204.2 ± 4.3	195-215	55	[2]6.67	111.7	0.000
Tail[1] (mm)	74.0 ± 3.2	66-80	58	79.6 ± 3.5	73-88	48	8.44	104	0.000
Total head (mm)	67.6 ± 2.0	62.8-71.4	61	69.0 ± 1.5	65.5-73.0	82	[2]4.64	108.2	0.000
Bill (mm)	28.4 ± 1.5	23.3-32.0	65	29.4 ± 1.3	26.4-32.5	89	4.76	152	0.000
Nalospi (mm)	17.3 ± 1.4	10.6-20.1	60	18.2 ± 0.8	15.9-20.1	78	[2]4.58	87.6	0.000
Tarsus+toe (mm)	82.9 ± 2.3	77-89	60	83.6 ± 2.5	78-89	85	1.79	143	0.076
Tarsus (mm)	48.0 ± 2.0	43.1-51.7	65	48.9 ± 1.8	44.5-52.7	89	2.89	152	0.004

[1] only adults from October to May with completed primary moult have been included.
[2] t-test for unequal variances.

Table 2. Measurements of first year birds divided in two temporal classes (September-November, December-May).

		Mean ± S.D.	Min-Max	n
Wing (mm)	Sept-Nov	197.1 ± 5.7	182-206	36
	Dec-May	198.8 ± 6.5	184-212	27
Tail (mm)	Sept-Nov	73.3 ± 2.9	66-79	32
	Dec-May	74.9 ± 3.4	68-80	26
Total head (mm)	Sept-Nov	67.1 ± 2.0	66.8-71.2	34
	Dec-May	68.2 ± 1.9	64.9-70.4	24
Bill (mm)	Sept-Nov	28.1 ± 1.6	23.3-32.0	38
	Dec-May	28.8 ± 1.3	26.6-30.9	27
Nalospi (mm)	Sept-Nov	17.0 ± 1.4	10.6-19.0	33
	Dec-May	17.8 ± 1.2	15.8-20.1	27
Tarsus (mm)	Sept-Nov	47.6 ± 2.1	43.1-51.5	38
	Dec-May	48.5 ± 1.8	44.7-51.7	27

Table 3. One-way ANOVA and Student-Newman-Keuls test (* = $p < 0.05$; - = NS) among measurements of adults (a) and first year birds divided in two temporal classes (c1= September-November, c2 = February-March) as in Tables 1 and 2, respectively.

	wing			tail			total head			bill			nalospi			tarsus		
ANOVA	$F_{2,107}$= 19.2 p< 0.0001			$F_{2,95}$= 36.5 p< 0.0001			$F_{2,152}$= 15.7 p< 0.0001			$F_{2,168}$= 13.8 p< 0.0001			$F_{2,146}$= 18.0 p< 0.0001			$F_{2,168}$= 3.9 p< 0.023		
S-N-K test	c1	c2	a	c1	c2	a	c1	c2	a	c1	c2	a	c1	c2	a	c1	c2	a
c1		-	*		-	*		*	*		*	*		*	*		-	*
c2			*			*			-			*			-			-

Table 4. Monthly body mass means of first-year and adult Grey Plovers. Significant mean differences between age categories obtained only in October (t-tests; t=3.86, df= 36.5, p< 0.001).

		Mean ± S.D.	Min-Max	n
August	first-years	-	-	-
	adults	205.8 ± 19.9	170.0-231.0	9
September	first-years	196.0 ± 14.3	183.0-212.0	3
	adults	210.9 ± 16.6	182.0-242.0	8
October	first-years	196.3 ± 20.7	157.0-233.5	23
	adults	215.7 ± 12.8	183.5-295.0	24
November	first-years	227.1 ± 33.2	178.0-275.0	12
	adults	235.8 ± 20.8	200.0-277.9	18
Dec.-February	first-years	253.2 ± 28.3	204.0-299.5	10
	adults	250.9 ± 22.9	205.0-315.0	29
March	first-years	232.8 ± 25.1	191.0-279.0	15
	adults	231.7 ± 22.4	201.0-276.0	15
April	first-years	-	-	-
	adults	190.0 ± 37.6	163.0-233.0	3
May	first-years	190.0 ± 32.5	167.0-213.0	2
	adults	238.0 ± 20.1	219.0-259.0	3

Table 5. Trapping dates and primary scores of second-year Grey Plovers. Figures in bold indicate those feathers that had been recently renewed during the post-juvenile primary moult and hence the presence of two primary generations. Scores according to Ginn & Melville (1983).

	Date	Primary score
1	5 July	3321000000
2	11 July	5432100000
3	14 August	5555555555
4	18 August	5555555555
5	18 August	5555555555
6	19 August	5555555555
7	30 August	5555555555
8	9 September	5555555555
9	21 September	5554420000
10	25 September	5555555554
11	11 October	5555555404
12	11 October	5540000000
13	16 October	5555555310
14	16 October	5555550000
15	19 October	5555500000
16	19 October	5555555421

Primary moult

No first-year birds were observed starting primary moult. Sixteen second-years were observed between July and October, their primary moult scores are shown in Table 5. By August and early September second-years had all already completed the primary moult and were in their first winter plumage. Six second-years showed two generations of new primaries, indicating the presence of two sequential primary moult cycles. These two cycles were found simultaneously active only in bird no. 11. Two birds, no. 10 and 16, indicated that the second cycle can be finished by November or earlier, while birds no. 14 and 15 were in arrested or suspended moult. All the observed second cycle moult stages except no. 12, were compatible in timing and scoring with the 'regular' post-breeding adult moult (Fig. 3).

Adult primary moult started in August (Fig. 3). Only four adults (all age 3y+) were trapped before the onset of primary moult, between 6-18 August, 46 were in active moult and 52 showed completed moult. The first adult with complete moult was observed on 5 October and the last one actively moulting on 21 December. Three birds out of 14 trapped in January-February were observed with primary moult suspended at p8. In March, nine out of 25 adults were resuming primary moult; the lowest observed point of moult resumption was p6. In April and May no adults out of six showed signs of suspension or active primary moult. The frequencies of suspended vs. completed moults in January-February and active vs. completed in March were not significantly different (χ^2 test). The estimate of the moult parameters for the adult autumn primary moult gave the following results: mean start 18 August (SE = 5.9), mean duration 93 days (SE = 8.1), mean closing day 19 November (SE = 4.1), standard deviation 21.8 (SE = 2.6).

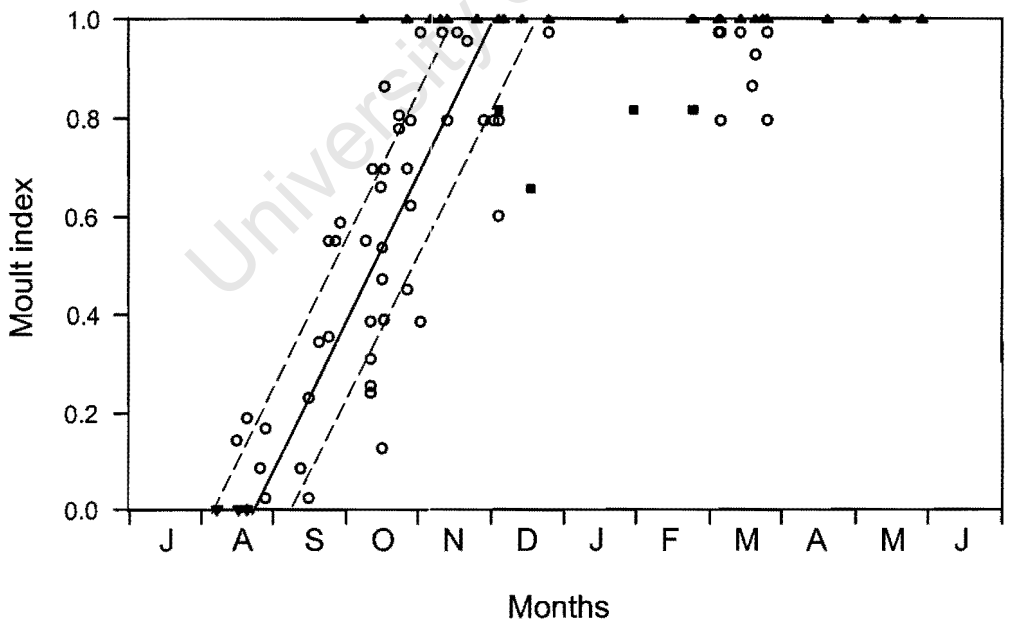

Fig. 3. Primary moult pattern of adult Grey Plovers in northeastern Italy. The solid line represents the estimated moult progression, dashed lines contain 95% of the population of active moulters. Open circles indicate birds in active moult, triangles birds before and after moult, solid squares birds with suspended moult. Birds in suspended moult or in active moult in March have not been used for the estimate of moult parameters (see Methods).

DISCUSSION

Biometrics and origin of birds

Mean wing length of adult Grey Plovers in northeastern Italy was 2.7% larger than those observed at the Wash, England, but the differences between the other available samples along the East Atlantic coast of Europe, Africa and India were all below (Table 6). Hence, wing length showed relatively slight differences on a wide geographical range of resting/wintering sites and does not appear to be a very useful measurement for investigating the breeding origin of wintering Grey Plovers (Engelmoer *et al.* 1987). Moreover, the observed geographical pattern of mean wing lengths does not reflect the expected cline of increasing means along a North-South axis, as could be supposed by the presence of such a gradient from West to East on Siberian breeding grounds (Glutz von Blotzheim *et al.* 1975, Cramp & Simmons 1983).

Table 6. Wing lengths of adult Grey Plovers from different parts of the non-breeding range. Percentages are referred to the Italian mean value of 204.2 mm.

		Mean ± S.D.	n	Period	Reference
England	-2.7%	198.8 ± 5.3	1124	August-May	BRANSON & MINTON 1976
Germany[1]	-1.2%	201.7 ± 5.1	227	April-May	PROKOSCH 1988
Tunisia	-0.2%	203.7 ± 7.3	115	March-May	SPIEKMAN *et al.* 1993
Egypt	-1.4%	201.4 ± 2.1	9	March-April	MEININGER & SCHEKKERMAN 1994
Mauritania[2]	-1.0%	202.0 ± 4.4	4	October	LENSINK & MEININGER 1990
Mauritania	-0.9%	202.4 ± 5.1	11	February-April	ENS *et al.* 1989
Guinea Bissau	-2.4%	199.4 ± 5.5	25	December-February	WYMENGA *et al.* 1992
India	-0.2%	203.8 ± 5.8	189	September-February	BALACHANDRAN *et al.* in press

[1] = males only but sex difference not significative
[2] = old primaries

The significant difference in wing length before and after moult provides further caution in the use of this measurement to separate populations (Pienkowski & Minton 1973). The lower abrasion rates between old and new primaries observed in England and India, both accounting for 0.5% of wing length, compared with 1.6% of this study, can be explained by the fact that we have introduced an upper date limit in December for the new feather bird category (Branson & Minton 1976, Balachandran *et al.* 2000).

Italian adult mean bill length was shorter than all the recorded samples from Palearctic wintering areas or passage sites (Table 7). From bill length it could therefore be supposed that Italian wintering Grey Plovers had a dominant component of western Siberian birds, being long-billed Grey Plovers considered to have eastern origins, but the geographical distribution of bill lengths seems far from clear and in disagreement with that suggested by wing length. Furthermore, the absence of recoveries linking Italy with the East Atlantic Flyway leads to hypothesise the use of distinct, more eastern routes for Italian Grey Plovers, and consequently also a more eastern origin.

First-years completed their feather growth by the end of November, but showed shorter mean wing and tail lengths than adults after this period. At the same time, total head, nalospi, tarsus+toe and tarsus lengths reached adult values, while bill length remained shorter than in adults, indicating that a longer period is required for reaching adult values. First-year mean bill length recorded at the German Wadden Sea during spring migration was still shorter than that of adults (29.3 vs. 29.8 mm), although not significantly (Prokosch 1988).

Table 7. Bill lengths of adult Grey Plovers from different parts of the non-breeding range. Percentages are referred to the Italian mean value of 29.4 mm.

		Mean ± S.D.	n	Period	Reference
England	+2.3%	30.1 ± 1.4	852	August-May	BRANSON & MINTON 1976
Germany[1]	+1.4%	29.8 ± 1.4	222	April-May	PROKOSCH 1988
Tunisia	+4.8%	30.8 ± 1.3	82	March-May	SPIEKMAN *et al.* 1993
Egypt	+0.7%	29.6 ± 1.1	9	March-April	MEININGER & SCHEKKERMAN 1994
Mauritania	+6.8%	31.4 ± 0.5	6	October	LENSINK & MEININGER 1990
Mauritania	+1.4%	29.8 ± 1.8	11	February-April	ENS *et al.* 1989
Guinea Bissau	+6.6%	31.5 ± 1.2	112	December-February	WYMENGA *et al.* 1992
India	+9.2%	32.1 ± 1.2	263	September-February	BALACHANDRAN *et al.* in press

[1] = males only but sex difference not significative

Body mass

The body mass pattern of adults over the period August to March closely resembled that observed at the Wash, i.e. distinctive of sites characterised by mid-winter fattening (Branson & Minton 1976), but monthly averages were constantly lower in Italy apart for March. Lower means before November in Italy might be explained by the presence of birds gaining weight at the Wash before embarking into a further migration step, but the winter peak difference, accounting for *c.* 30 g, is probably related to different local stress factors such as food availability and weather conditions (Johnson 1985). In spring, pre-migratory body mass increase was not evident at our study area, possibly because birds moved early in the season towards other sites located within a distance they can reach without carrying heavy energy loads. Similar movements are probably performed by Dunlins *Calidris alpina* wintering in Tunisia (Spiekman *et al.* 1993) and also by other arctic wader species wintering in the west Mediterranean.

First-years showed the same temporal body mass variation of adults, accordingly to the same pattern described for first-years wintering at the Wash (Branson & Minton 1976). In northeastern Italy, the two age categories had similar mass values from November onwards, while in England adults were *c.* 40 g heavier than first-years at December peak. Energy reserves are highly regulated by birds, directly responding to local conditions: higher reserves at increasing risks. Age-related differences in body reserves at mid-winter peak are well known for waders and have been interpreted as an indication of different feeding efficiency or resource exploitation (Johnson 1985). The fact that adults and first-years at our study area respond in the same way to weather stress suggests that age-related differences can be interpreted only at local level and not as a general feature of the species.

Primary moult

Adults started primary moult soon after their arrival in August and there was no indication of further immigration into the area after the end of September, when 95% of the population had started the moult. The low number of birds trapped before the onset of moult can be explained by its rapid start once the birds have reached the wintering site. A pressure for an immediate start of the moult can be easily explained as an adaptment to a relatively short time for moulting between the relatively late settlement in the moulting areas and

the arrival of severe weather conditions (Boere 1976). The absence of birds in suspended primary moult at its earlier stages, in contrast with the observations from Morocco (Pienkowski *et al.* 1976), the Wadden Sea (Boere 1976) or the Wash, where the migrant turn-over was high and suspended birds accounted for 25-40% of the population in August (Branson & Minton 1976), might indicate that emigration, at least during moult period, was negligible. The arrival of birds in suspended moult, quickly resuming it after having settled, cannot be excluded, but their proportion must be very low. The same can be assumed for active migrants with open moult, because migration and moult are mutually exclusive processes in waders performing long non-stop flights, as the Grey Plover does (Koopman 1986, Zwarts *et al.* 1990, Piersma & Jukema 1993).

Advanced points of primary moult suspension were observed only after the end of November, when last moulters can possibly be forced to discontinue moult by the incoming winter season, although one bird was found completing the growth of the outermost primary on 21 December. Moult resumption was observed only in March (from mid-March at the Wash) and no suspended birds were found during spring months, suggesting that pre-breeding migration follows primary moult completion.

The estimated mean duration of 93 days for adults which did not interrupt the autumn moult fits to the 90 and 90-100 days calculated for the Wash, England, and the Dutch Wadden Sea, despite the different methods used for obtaining these estimates; moult periods were also almost synchronous at these three sites (Boere 1976, Branson & Minton 1976). Moult in northeastern Italy was faster than in India, where starting date and moult duration calculated using the same statistical model were 1 September and 127 days, respectively (Balachandran *et al.* in press). If the difference in moult timing can at least be partly explained in terms of distance from the breeding grounds and the date of arrival in the moulting area, then the different duration of moult could be attributed, at the individual level, to a lower moult speed. A prolongation of moult period from northern to southern wintering sites has been described for several wader species and it is generally linked with the 'benign' nature of the climate in the wintering area (Pienkowski *et al.* 1976, Summers *et al.* 1989, Marks 1993).

The first cycle of second-year primary moult cannot be described by our data, it only appeared that it was usually completed by the end of August, as observed in northern Europe (Boere 1976, Branson & Minton 1976). The presence of a second sequential cycle, in some cases concurrently active with the first, as well as the pre-winter suspension of this second cycle, was previously described for the Wadden Sea and Morocco, though it was explained as a resumption of the post-breeding primary moult of the previous year (Boere 1976, Pienkowski *et al.* 1976). Our data instead referred only to second-years, as in India (Balachandran *et al.* in press). The absence of retained old primaries among adults at their arrival in Italy after the post-breeding migration could be linked to the presence of a longer period with favourable conditions before pre-breeding movements than in northern Europe, allowing a greater proportion of winter suspended birds to complete their moult. We do not have direct evidence whether suspended cycles of second-years are resumed at the end of the winter, although the absence of birds with suspended moult from March would lead to assume that they generally complete the cycle.

Timing of presence and site fidelity

Adult Grey Plovers settled in the study area from the beginning of August to mid September, first-years appearing only from September. Local retraps indicated that at least a part of the wintering population did not leave the area until March, although there is some evidence from spring resumed primary moult that some birds could move earlier. Late winter movement and pre-migration gathering sites have been described from different

parts of the wintering range (Casini *et al.* 1992, Liversidge *et al.* 1958, Martinez Vilalta 1985, Motis *et al.* 1981) but there are no indications to speculate further yet. The high proportion of local retraps from year to year and the absence of recoveries from other wintering sites indicated a strong site fidelity. Besides the overwintering population, the presence of migrants using the area as a stop-over site during southward migration was confirmed by an August recovery of a South African ringed bird, and the passage of birds heading to the breeding grounds in spring was suggested by some lean birds caught in April and May.

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CHAPTER 4

MOULT AND MIGRATION OF GREY PLOVERS *PLUVIALIS SQUATAROLA* WINTERING IN SOUTH AFRICA

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Data on 355 Grey Plovers Pluvialis squatarola *trapped in South Africa in 1971-1997 were used to describe seasonal body mass variation and moult in relation to their very long migrations. The estimated duration of adult primary moult, 131 days, was similar to that observed in India and 30-40 days shorter than durations reported for localities in Europe. All first/second-year birds oversummering in South Africa underwent a complete moult between their first boreal spring and second boreal summer. The presence of two concurrent or consecutive primary moult cycles was observed in 35% of second-years. It is suggested that the primary moult of first/second-years might be considered as an anticipated post-breeding moult rather than a postponement of the post-juvenile body moult or a delayed pre-migratory one. If this hypothesis were confirmed, the second primary moult cycle observed in oversummering first-year Grey Plovers would be a supplemental post-breeding moult. This cycle might have no adaptive value and occur through the absence of endogenous cues which stop the moult. Pre-migratory mass gain was observed only in birds which had completed or suspended primary moult. Individual departure values (> 310 g) were reached from 15 March, but most birds departed between 15-30 April. Grey Plovers left South Africa before having moulted into a complete breeding plumage.*

INTRODUCTION

To shed light on various aspects of the ecology of migrant waders, seasonal body mass variation has been widely studied in relation to migration and moult of contour and flight feathers (e.g. Pearson 1981, 1987, Johnson *et al.* 1989, Summers *et al.* 1989, Zwarts *et al.* 1990, Marks 1993, Piersma & Jukema 1993). Data collected at the extreme limits of a species' geographical distribution are of great heuristic value because such areas generally, or predominantly, host single populations and therefore present simplified situations (Thomas & Dartnall 1971, Tree 1977, 1979, Elliott *et al.* 1976, Waltner & Sinclair 1981, Summers *et al.* 1987a, 1989, Summers & Waltner 1989, Balachandran *et al.* in press). In the Afro-Palearctic migratory system, 20 species of Palearctic waders have their southern distributional limit in South Africa (Harrison *et al.* 1997). Among them is the Grey Plover *Pluvialis squatarola*. It breeds in the High Arctic and performs biannual migration journeys between summer and winter ranges, covering long distances by non-stop flights. South Africa has a population of *c.* 8800 Grey Plovers, occurring mainly along the Atlantic coast (Summers *et al.* 1987b, Underhill 1997).

This paper aims to describe seasonal body mass variation, moult and migration movements of South African Grey Plovers through the analysis of biometric, moult and plumage data. These results provide a

framework for discussing moult and migration strategies adopted by this species and other waders wintering at subtropical latitudes.

STUDY AREA AND METHODS

Data from 355 Grey Plovers caught in South Africa in 1971-1997, were analysed. Seventy-five percent of birds were trapped at Langebaan Lagoon (33°12'S, 18°07'E) and 16% at Swartkops River estuary (33°45'S, 25°38'E); other sites accounted for 0.1-3.4%. Grey Plovers were mainly trapped in mist-nets at or close to high-tide roosts; only a minority was caught by cannon-nets or dazzling.

Birds were aged according to plumage characters (Prater *et al.* 1979, Cramp & Simmons 1983) and divided into the following categories: first-years (birds in their first year of life, from their arrival in juvenile plumage in October-November to 30 June), second-years (birds in their second year, from 1 July to the completion of their first primary moult in October-November) and adults (birds older than first-years, from arrival from breeding grounds in August to departure in April). Second-years were always excluded from adult category when identified, but ageing was problematic towards the end of the first primary moult, when juvenile feathers retained from the post-juvenile partial moult (some tertials, scapulars, rump and wing coverts) were lost. However, looking at the more advanced stage of the juvenile primary moult in comparison to the timing of adult moult and the presence of juvenile primaries (more pointed, faded and abraded than adult primaries), the number of unaged birds was greatly reduced.

Body mass was recorded with spring balances to the nearest gram. No correction indices for body mass loss could be applied, because the time gap between bird catching and measuring was seldom registered, even if it was generally less than one hour.

Primaries were numbered from innermost (P1) to outermost (P10). Primary moult scores were recorded (Ginn & Melville 1983) and converted to percentage feather mass grown (Underhill & Joubert 1995). Moult parameters were estimated using the statistical method of Underhill & Zucchini (1988). This method considers three types of data, in relation to different scenarios of bird presence in the study area and sampling techniques, later supplemented with two more data types (Underhill *et al.* 1990). Our data fulfil the conditions of type 2 because adult Grey Plovers arrive in South Africa with the full set of old primaries, moult and then stay till pre-breeding migration. Some second-years showed two concurrent cycles of primary moult. In such birds, moult parameters were estimated separately for each of the two moult cycles. We assumed therefore that moult speed and pattern were not different in birds with one or two cycles.

The presence of breeding plumage was recorded in the field on a scale of 0 (full winter plumage) to 8 (full breeding plumage), or in percentage of breeding plumage. In the analysis, due to the small number of birds checked for plumage and different scales adopted, the following categories of percentage of breeding plumage were used: 0 = 0%, 1 = 1-28%, 2 = 29-56%, 3 = 57-84%, 4 = 85-100%.

Except where stated, seasons refer to the northern hemisphere. In some cases, dates were converted to days and numbered from 1 July to 30 June. Because the cycles of many biological events, such as juvenile primary moult or body mass variations, crossed over the year limit set at 30 June, dates of the second year were made additive.

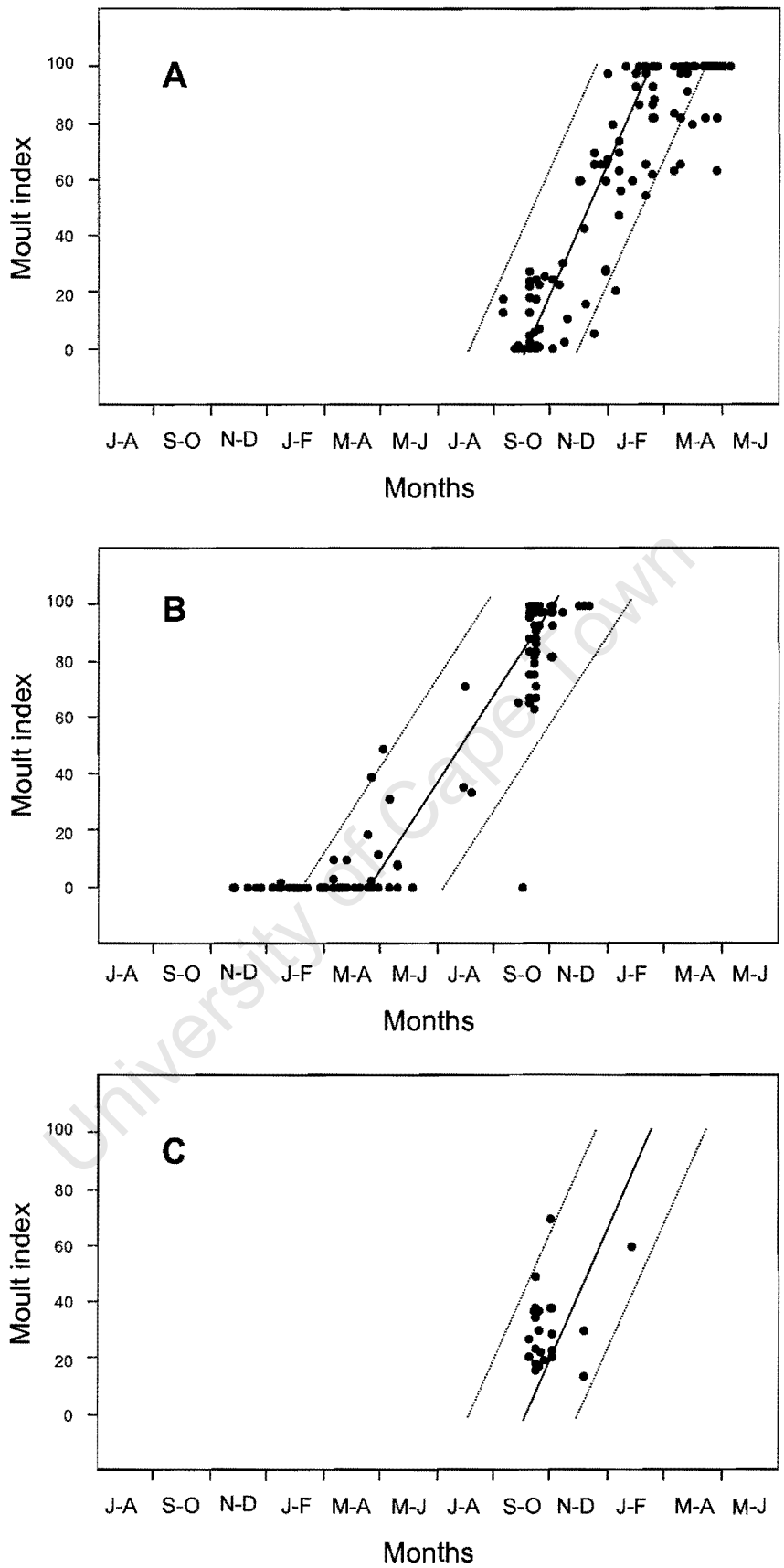

Fig. 1. Seasonal distribution of primary moult indices based on percentage feather mass grown. The solid lines represent the estimated moult progression for the average bird, the dashed lines delimit the areas where *c.* 95% of each population is included. A = primary moult in adults, B = first cycle of primary moult in first/second year birds, C = second cycle of primary moult in second-year birds. Due to the low number of cases, moult parameters for the second cycle have not been calculated, the parallelogram of adult moult is showed for comparison.

RESULTS

Moult of primaries and contour feathers

No adult birds with active or suspended primary moult were observed on arrival in South Africa, suggesting that primary moult usually started after they had settled in September-October (Fig. 1a). The estimated duration for adult primary moult was 131 days (SD = 6), from 30 September (SD = 6) to 8 February (SD = 4). The parameter of the variance in moult duration (the 'standard deviation parameter' of Underhill & Zucchini 1988) was estimated at 28 days, with a SD of 2. Three adults were found in suspended primary moult, one in February and two in April, all with the outermost primary retained. The same pattern, but with the outer two primaries from the previous generation, was observed on a bird caught in November.

In first-year birds, the first observation of primary moult was on 10 January and the last one on 4 November of the second year (Fig. 1b). The estimated duration of primary moult was 194 days (SD = 9), from 19 April (SD = 7) to 20 October (SD = 6). The estimate of the standard deviation parameter was 36 days (SD = 6).

Twenty-four second-year birds (35%) showed two cycles of primary moult, and in 16 (24%) these were simultaneously active. In birds observed with two active moult cycles, the first cycle had invariably reached the same stage (P10 was growing), but the second cycle ranged from P2 to P9 (mean = 4.6, SD = 1.4). Timing of the second cycle overlapped adult primary moult (Fig. 1c).

In September, less than 10% of adults were still in full breeding plumage, and most birds showed transitional plumage stages (Fig. 2). From October, birds completed body moult and attained a full non-breeding plumage. From February, soon after they had completed primary moult, adults started to moult into breeding plumage. No birds were seen in full breeding plumage in April, the latest period of their stay in South Africa (Underhill 1997). Of 12 first-years examined in March-June, none had any breeding plumage feathers, of 18 second-years examined in July-October, three (17%) showed traces of breeding plumage. Among the latter, one caught on 19 September had 45% of breeding plumage and had just started juvenile primary moult (primary score: 1110000000).

Seasonal phenology of body mass

From October to April, adults in active primary moult averaged 214 g. Body mass did not vary among these months (one-way ANOVA, $F_{6,76} = 0.44$, NS). In January and February, birds which had finished primary moult were heavier than birds in moult, and averaged 233 g (n = 6, SD = 16) and 229 g (n = 11, SD = 39), respectively. Evidence of a pre-migratory body mass increase was observed in March (average 260 g, n = 49, SD = 33) and April (average 301 g, n = 60, SD = 24; Fig. 3). Assuming that the average mass of moulting birds represents the initial mass, and that the average mass of the upper half of the frequency distribution of birds caught during the fattening period (March-April), 310 g, represents minimal departure mass (Zwarts *et al.* 1990), body mass increased approximately 45% (96 g). Birds that reached the threshold of 310 g, and were thus ready to start migration, were regularly found from 15 March to 30 April (Fig. 4). Their proportion was around 20% between 15 March and 15 April, indicating that the number of newly moulted birds, ready to prepare for migration, equalled that of birds which had reached migratory values and had left. The significant increase in the proportion of birds ready to take off in the last 15 days of April (60%) suggested that the recruitment of birds for migration was completed.

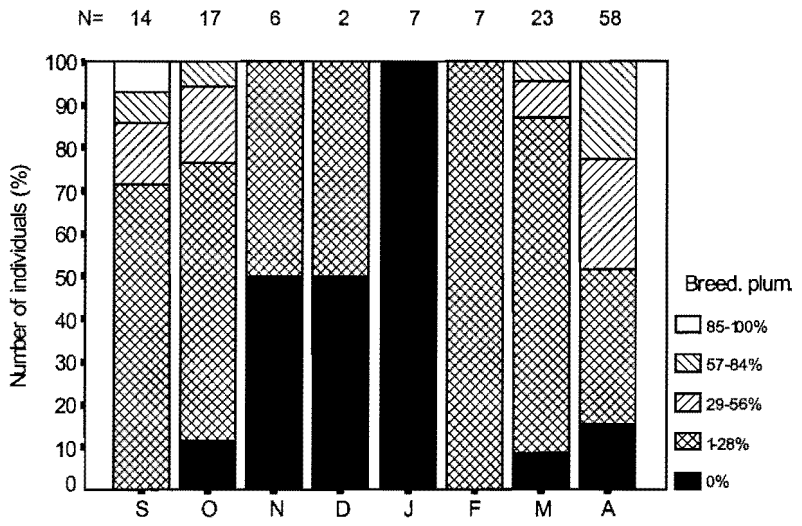

Fig. 2. Monthly distribution of plumage categories in adult Grey Plovers.

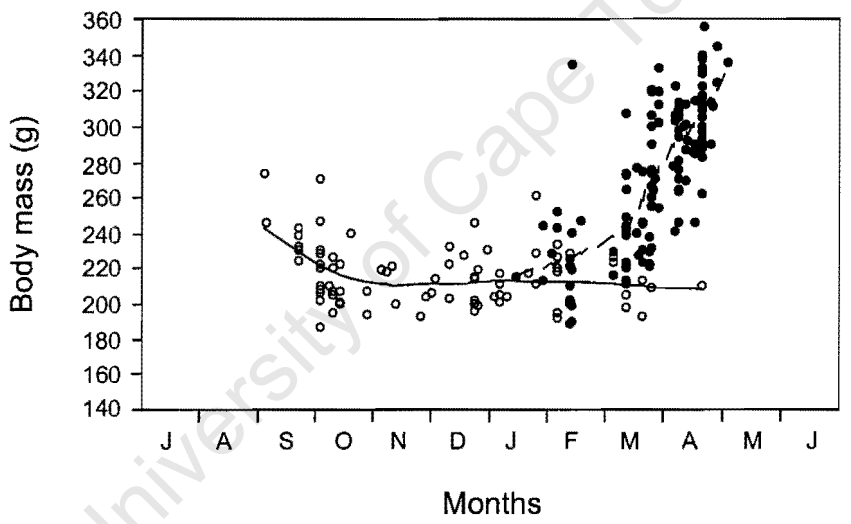

Fig. 3. Seasonal distribution of body mass values for adults. The lines represent Lowess-regressions fitted to 50% of the points.

Considering the strict relationship between the end of primary moult and the onset of pre-migratory fattening (Fig. 3), and the observation that about 95% of the adult population had finished primary moult by 4 April (Fig. 1a), we assumed this date as the latest one on which birds started to gain body mass. These late birds had no more then 26 days to reach pre-migratory values by 30 April. If body mass was gained at a constant daily rate, a minimum increase rate of 3.7 g/day (1.7% of the initial mass) was required. These results are similar to those obtained by a linear regression of days taken as the independent variable on body mass (period considered: 1 March-30 April; $F_{1,107} = 102.3$, $P < 0.0001$; $r^2 = 0.49$; B = 0.3 ± 0.03; constant = 187.6 ± 8.5, $P < 0.0001$) which estimates an increase rate of 3.5 g/day and 28 days for reaching take-off values.

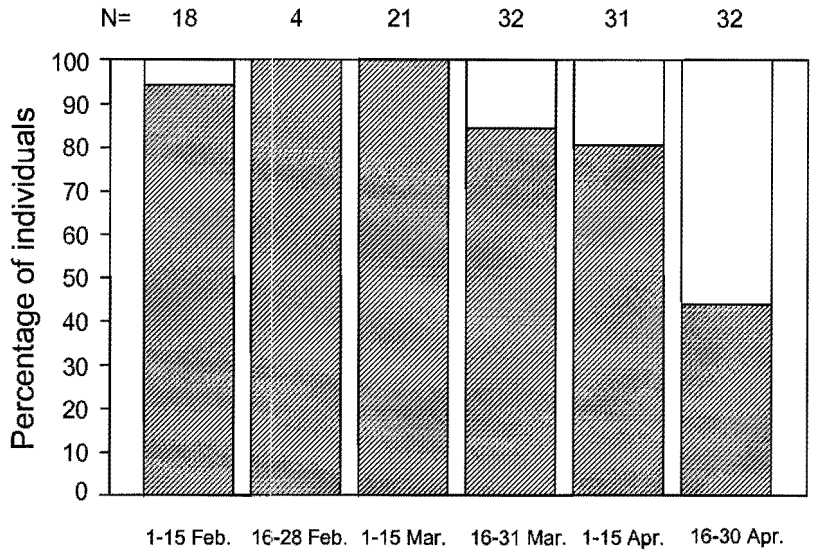

Fig. 4. Frequency distribution of adults ready to take off (empty bars) and still gaining mass (hatched bars) against time. The first birds which reached the take-off threshold of 310 g appeared in February, but they were regularly present only since 16 March. After mid-April they outnumbered birds still gaining mass.

Mean body mass of adults preparing for migration (i.e. considering only birds with new primaries) did not vary significantly when divided into categories of percentage of attained breeding plumage (one-way ANOVA, $F_{3,66} = 0.55$, NS).

First-year birds weighed less than adults upon their arrival in September-December, averaging 184 g vs. 216 g of adults (*t*-test = 4.6, $df = 71$, $P < 0.0001$). Their body mass increased slowly throughout the winter, maintaining lower values than adults till May (Fig. 5a). Between January and March, the distribution of body masses was positively skewed (median = 204 g, mean = 213 g, SD = 28.7, skewness= 0.77, SE of skewness = 0.38, $n = 38$). Twenty-five percent of the first-years were heavier than 230 g (mean value of non-moulting adults in that period), suggesting that some first-years put on energy stores during the austral summer (Fig. 5b). However, none of them reached pre-migratory values. Second-year birds averaged 211.5 g (SD = 13.0, range 183-244, $n = 56$) and did not show significant variation from July to December (ANOVA, $F_{4,51} = 0.599$, NS).

DISCUSSION

Primary moult

The onset of primary moult during the last phases of the breeding season has been reported from various sectors along the species' Palearctic range and it probably involves mainly males (Hötker 1995, Gromadzka & Serra 1998). The proportion of birds showing signs of this early start of the moult varies at different stopover sites or wintering areas. At the Wash, England, 25-40% of adults had replaced from one to three primaries upon arrival in August (Branson & Minton 1976), and 11% in the southern Baltic (Gromadzka & Serra 1998). Grey Plovers in South Africa did not present any indication of such suspension, as recorded in Italy and India (Serra & Rusticali 1998, Balachandran *et al.* in press). The absence of such observations at sites where mainly wintering birds are present, might be due to the prompt resumption of moult once they have settled, and the low proportion of birds

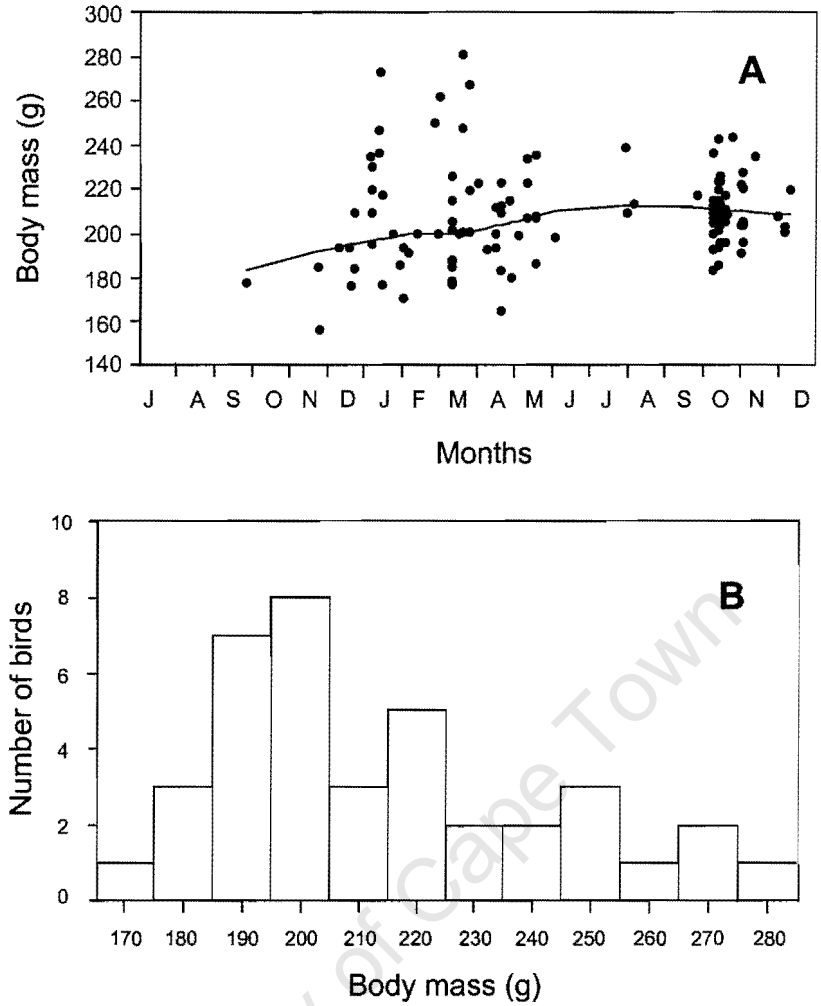

Fig. 5. (A) Seasonal distribution of body masses of first- and second-year birds. The line represents a Lowess-regression fitted to 50% of the points. (B) Frequency distribution of body mass of first-year birds caught between January and March. The skewed curve indicates that *c.* 25% of the birds were gaining mass.

caught with the full set of old primaries - at all the sites mentioned above - might support this hypothesis. However, as the sex-ratio is probably not balanced in winter quarters, with females outnumbering males in the southern part (Cramp & Simmons 1983), the higher proportion of females at the southern edge of Africa could contribute to explain this pattern.

On the winter quarters, moult duration varies from 90-100 days in England (Branson & Minton 1976), Dutch Wadden Sea (Boere 1976) and Italy (Serra & Rusticali 1998) to 127-131 days in India (Balachandran *et al.* in press) and South Africa. The existence of a distributional limit at *c.* 20° latitude North, which possibly separates populations forced by local conditions to moult at maximum speed from others which are not constrained by the onset of a cold winter season and can therefore moult at an optimal speed for producing high-quality flight feathers, was suggested to explain the presence of this geographical pattern of moult durations (Serra 1998). Adult Grey Plovers encounter benign conditions in South Africa. This allows them to moult during their whole period of presence, apart from the 3-4 weeks which precede departure. Despite the long season available for moulting, a small fraction of South African birds did not complete primary moult before migration, in contrast with what was observed in India, where all adults moved northward with a full set of new primaries.

However, the onset of moult in India is estimated as 1 September (Balachandran *et al.* in press), about 30 days earlier than in South Africa. The longer time required by Grey Plovers to reach South Africa may restrict the available period for moulting; birds that settle late in the season may not be able to complete moult before departure date. Grey Plovers wintering at the two latitudinal extremes of their Afro-Palearctic range might therefore converge on a similar strategy in order to solve time constraints of different kinds.

Apparently, all first/second-years spending the boreal summer in South Africa moult primaries between their first spring and second summer, giving clear indication that they will not return to the breeding grounds in that season. Primary moult of oversummering Grey Plovers has not been studied in detail elsewhere. Available data suggest that the start of moult is probably deferred until May-June in the Mediterranean and northwestern Europe, and moult completion is likely to occur in August-September (Branson & Minton 1976, Prokosch 1988, Serra & Rusticali 1998). This different moult timing could be linked to the longer period of presence of adults and more severe winter conditions at northern latitudes. Resource availability and competition with adults have been invoked as factors affecting moult timing in first-year American and Pacific Golden Plovers *Pluvialis dominica* and *Pluvialis fulva* (O.W. Johnson 1985), Sanderling (Myers *et al.* 1985) and Bristle-thighed Curlew *Numenius tahitiensis* (Marks 1993). As a rule, first-years settled on wintering sites some weeks later than adults and could have difficulty in maintaining an optimal energy budget in an environment not previously visited and already occupied by adults (O.W. Johnson 1985). This scenario is appropriate for Grey Plovers because differential timing of settlement, lower body masses in first-years and intra-specific competion have been found at South African estuaries (Turpie & Hockey 1996), and also at the northern limit of the winter range (C. Johnson 1985, Townshend 1985). This suggests that inexperienced first-year Grey Plovers might have a limited access to food resources, and thus be driven to perform juvenile primary moult when adults are absent. However, this hypothesis does not explain why there is not complete segregation between juvenile primary moult and adult presence, given that there are no time constraints for moulting in South Africa. First-years started moulting in South Africa when adults were gaining mass, i.e. when competition for resources should have been at maximum, and the same seems to happen in Europe (Prokosch 1988).

If the lack of a pre-migratory primary moult cannot be considered *per se* as a factor precluding northward migration in first-years (O.W. Johnson 1985), it is nevertheless evident that the norm for Palearctic waders which winter in subtropical Africa and migrate in their first year is to undergo a complete moult of primaries or to change the outermost ones (Pearson 1974, 1977, 1981, 1984, Tree 1974, 1977, Elliott *et al.* 1976, Dean 1977, Prater 1981, Waltner & Sinclair 1981). It seems therefore that for waders travelling long distances, there is a direct relation between an early moult of primaries and migration, or, conversely, between late moult and oversummering. Chu (1994) proposed that retention of juvenile primaries in the first year was a primitive character of the wader ancestor. If this is the case, then a selective pressure should operate on arctic wader population wintering in the southern hemisphere, driving species which breed in their first year to perform a partial or complete pre-migratory primary moult (supplemental moult *sensu* Prater 1981) during their first winter, in order to migrate with new primaries.

If the advantage of moulting when intraspecific competition is at a minimum appears rather obvious for birds which are not compelled to migrate by breeding, the relationship between the juvenile primary moult and the second, often concurrent cycle of primary moult, which replaces feathers which have just finished growing, remains obscure. Perhaps, during the austral winter Grey Plovers - and other arctic waders - do not face

ecological conditions severe enough to inhibit the start of the second cycle, as suggested for the Bristle-thighed Curlew in the Hawaii (Marks 1993).

As other long-distance migrants, the seasonal timing of migration, breeding and moult of Grey Plovers are likely to be subject to endogenous control and strictly linked one to each other (Berthold 1985, 1996). First-years that do not attain full breeding plumage, and do not migrate and breed, might not encounter physiological barriers to moulting. Levels of sex-steroid hormones, which are probably low in oversummering Grey Plovers, might play an important role in the lack of inhibition of the post-breeding moult (Hahn *et al.* 1992). If return to the breeding grounds and no primary moult in the first year of life were the ancestral conditions for waders (Chu 1994), the juvenile primary moult of oversummering Grey Plovers should be considered as an anticipated first post-breeding moult rather than a delayed phase of the post-juvenile moult. This hypothesis is supported by the fact that the post-juvenile body moult is finished before the onset of the juvenile primary moult (4-5 months before in Europe and North America), and the existence of a small proportion of first/second-year Grey Plovers attaining breeding plumage and delaying juvenile primary moult to adult timing (Paulson 1995). Following this line of reasoning, the second primary moult cycle in oversummering birds might be considered as a supplemental post-breeding moult and proceed till the switching on of endogenous cues which stop the moult, operated by signals like the onset of unfavourable conditions or pre-migratory fattening (Hahn *et al.* 1992, Berthold 1996). This second cycle might have no adaptive value.

Body mass and migrations

Premigratory fattening was observed in adults which had completed or suspended primary moult, while adults in active moult and most first-years did not gain mass. Our estimate of an 'individual' daily increase rate of 1.7% falls close the range of 1.0-1.5% calculated for populations of other waders preparing for migration in South Africa (Middlemiss 1961, Elliott *et al.* 1976, Summers *et al.* 1987a, 1989, Summers & Waltner 1979) and to the 1.8% observed in Grey Plovers wintering in Britain (Branson & Minton 1976). These values are far from the average daily mass increase of 3.5% at the German Wadden Sea in spring (Prokosch 1988) and from the maximum theoretical rates of *c.* 4-5% calculated for waders (Zwarts *et al.* 1990). Zwarts *et al.* (1990) pointed out that fattening rates of waders at wintering sites may be underestimated, because mean mass are biased downwards by prolonged departure periods and variable increase rates. Nevertheless, besides methodological limits, two possible biological reasons why waders do not gain mass at the maximum rate of metabolizable energy intake have been suggested (Zwarts *et al.* 1990): (a) the advantage of carrying extra fat loads for the shortest possible period does not balance the risk of missing the body mass departure value at the latest possible departure date; (b) food conditions are poor and do not allow mass gain at the maximum metabolic rate. However, there are indications that food conditions play only a minor role as short-term factors, because birds are able - to some extent - to compensate for food reductions by increasing foraging activity, and inter-annual variations in food supply are not correlated with changes in the increase rates (Zwarts *et al.* 1990, Biebach 1996). Average feeding conditions seem therefore to act in the longer term, on the evolution of increase rates at population level (Zwarts *et al.* 1990).

Departure values of body mass were observed not only in birds at the final stages of pre-breeding body moult, but also in birds at initial stages of body moult or before it. Grey Plovers seem therefore to leave South Africa before completing moult into a breeding plumage, showing as wide a range of plumages at departure as in Guinea-Bissau (Ruiters & Fokker 1998) and Venezuela (McNeil 1970). That waders in full breeding plumage

have greater body masses than birds at earlier stages has been described for various species and at different wintering areas (O.W. Johnson 1985, Pearson 1987, Zwarts *et al.* 1990, Morrison & Harrington 1992). It appears that at sites located at closer distances to breeding grounds, where the onset of migration can be delayed, higher proportions of waders complete the pre-breeding body moult. In South Africa, the time scheduling of post-breeding moult and departure would not allow pre-breeding body moult to be completed. In this case, the urge of moving northward seems to be stronger than that of attaining a full breeding plumage.

Adults appeared ready to leave for northward migration from 15 March, but the bulk of departures were between 15-30 April. This time schedule fits the pattern of presence obtained from census data at three of the most important South African wetlands, that all featured an abrupt numeric decrease between April and May (Taylor 1956, Liversidge *et al.* 1958, Pringle & Cooper 1975, Martin & Baird 1987, Spearpoint *et al.* 1988, Velasquez *et al.* 1991).

A small fraction of first-year birds gained mass between January and March, apparently in contrast to findings from the Siberian breeding grounds, where first breeding attempts are thought not to occur before age 2-3 years (Cramp & Simmons 1983). However, fat first-years were observed on northward migration in North America, and specimens from American breeding grounds were aged as first-years, establishing that breeding may take place at this age (Paulson 1995). Carrying extra fat loads is costly and therefore avoided if not strictly necessary (Houston & McNamara 1993, Gosler *et al.* 1995, Pilastro *et al.* 1995). Even though first-year body mass gain occurred earlier in the season in respect to timing of adult fattening, and adult pre-migratory body mass values were not reached, *c.* 25% of first-years prepared for an energy demanding event. They could use these stores either to migrate towards sites which offer better conditions for moulting - such as Langebaan Lagoon, Berg River or Swartkops estuaries - and adapt to the new environment, or embark on longer, transcontinental journeys. There is evidence for both movements: a colour-ringed first-year bird, marked at Port Alfred, Eastern Cape, on 29 March 1992 was observed 121 km west at Swartkops estuary on 13 July 1992 (A.J.T. pers. comm.) and a first-year ringed at Walvis Bay, Namibia, in March 1975 was recovered the following August in Crimea, Ukraine (Underhill 1997). In northern Europe, a small and highly variable proportion of first-year Grey Plovers oversummer, suggesting that a return to the breeding quarters when the birds are one year old occurs regularly (Boere 1976, Prokosch 1988, Summers *et al.* 1997). In South Africa, more than 10,000 Km further away from the breeding grounds, most birds stay put until two years old. Yet, some first-year Grey Plovers may nevertheless initiate northward migration.

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CHAPTER 5

BIOMETRICS, POSSIBLE BREEDING ORIGINS AND MIGRATION ROUTES OF SOUTH-AFRICAN GREY PLOVERS *PLUVIALIS SQUATAROLA*

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Data on 355 Grey Plovers Pluvialis squatarola *ringed in South Africa in 1971-1997 were analysed. Biometrics could not identify well-defined origins in the Siberian breeding grounds, but suggested the presence of birds from east of the Gydan Peninsula. Comparisons with populations spending the non-breeding period elsewhere did not allow a clear definition of the flyways used, although ringing recoveries indicated a migration route crossing the Mediterranean/Black Sea Region during both southward and northward movements. First-year birds were on average smaller than adults. Bill length increased during the first year, reaching adult length by June. First-year wing length decreased by 4% before the outermost primary was shed, adult wing length did not change with season.*

INTRODUCTION

Our knowledge about migrations and breeding origins of South African Grey Plovers *Pluvialis squatarola* is poor, although this is one of the commonest Palearctic waders in the region. South Africa has a population of *c.* 8 800 individuals, mainly distributed along the Atlantic coast (Summers *et al.* 1987a, Underhill 1997). Grey Plovers are present at South African wetlands throughout the year, because most first-years do not migrate until their second year of life (Summers *et al.* 1995, Serra *et al.* 1999). Numbers peak in November-March, when adults are present (Underhill 1997).

Links between breeding grounds, stopover sites and non-breeding areas are poorly known because ringing recoveries are few and geographical populations not clearly characterised (Cramp & Simmons 1983, Engelmoer & Roselaar 1998). Until new techniques for tracking bird movements become available, biometric comparisons and ringing recovery analyses represent the most useful tools for identifying bird origins and movements, despite the fact that morphometrical analyses are problematic in some species, such as the Grey Plover, due to slight sexual and geographical size variations (Tomkovich & Serra 1999).

In this paper, we analyse morphometrical and ringing data of South African Grey Plovers in relation to available information from other non-breeding areas and suggest possible origins and migration routes. Complementary information on migration, moult and seasonal body mass variation obtained from the same dataset has been presented in a previous paper (Serra *et al.* 1999). Methodological limitations to biometric comparisons arising from age-related and seasonal variations of wing and bill lengths also are described.

STUDY AREA AND METHODS

Between 1971 and 1997, Grey Plovers were ringed at nine sites in South Africa, mainly along the Atlantic coast (Fig. 1). Birds were aged according to plumage characters (Prater *et al.* 1979, Cramp & Simmons 1983) and divided into the following categories: first-year birds (birds in their first year of life, from their arrival in juvenile plumage in October-November to 30 June of the following year), second-year birds (birds in their second year, from 1 July to the completion of their first moult in October-November of the same year) and adults (birds older than first-years, from arrival from breeding grounds in August to departure in April). Second-year birds were always excluded from adult category when identified. Measurements regularly taken were maximum wing length, bill length from feathering and tail and tarsus lengths to the nearest mm (Prater *et al.* 1979).

Where not otherwise stated, seasons refer to the southern hemisphere. Dates were converted to days and numbered from 1 July to 30 June. Because many biological events, such as bill growth or body mass variations, crossed over the year limit set at 30 June, dates of the second year were made additive.

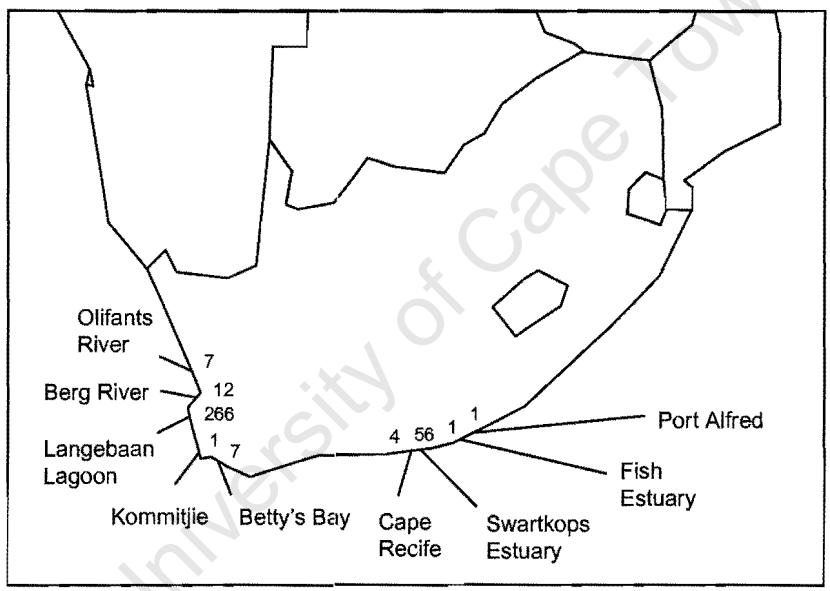

Fig. 1. Map of South Africa showing ringing sites and numbers of ringed birds.

RESULTS

In total, 355 Grey Plovers were caught (68 first-year birds, 57 second-year birds and 230 adults). Seventy-five percent of birds were ringed at Langebaan Lagoon and 16% at Swartkops River estuary; other sites accounted for 0.3-3.4% each. Four of them were recovered abroad and one foreign-ringed bird was retrapped in South Africa (Table 1). No Grey Plovers were recaptured at the ringing site or elsewhere in South Africa, apart from a single first-year bird ringed on 25 June 1986 at Amsterdamhoek, Port Elizabeth (33°51'S, 25°36'E), and found dead seven months later 3 km from the ringing site.

Adult mean wing length did not change before and after primary moult (t_{194} = 1.3, NS; Table 2), and there was no seasonal variation of wing length of moulted birds between the end of the moult and the onset of pre-breeding migration (Table 3). First-year birds had wing length 3.7% shorter than adults when outer primaries were not abraded.

Table 1. Details of ringing recoveries connecting South Africa to other countries.

Ring	Age	Date	Site		Direction	Distance (km)
D06020	adult	7.2.1981	Geelbek Marshes, SA	33°12'S-18°07'E	357°	8620
		20.8.1985	Savio River mouth, Italy	44°19'N-12.20'E		
D06031	2 year	25.10.1981	Geelbek, SA	33°10'S-18°04'E	10°	8928
		26.5.1997	Dzhankoy, Ukraine	45°47'N-34°31'E		
D06055	1 year	13.2.1983	Geelbek Marshes, SA	33°12'S-18°07'E	9°	9005
		10.9.1992	Vysokoe, Ukraine	46°50'N-32°21'E		
D19773	1 year	13.01.1988	Geelbek Marshes, SA	33°12'S-18°07'E	10°	8928
		29.08.1995	Dzhankoy, Ukraine	45°48'N-34°30'E		
P5681	adult	18.10.1969	Dobrudje, Romania	45°35'N-28°42'E	181°	8849
		23.8.1970[1]	Cape Recife, SA	34°02'S-25°42'E		

[1] Date of recovery, date of death unknown.

Table 2. Measurements of Grey Plovers ringed in South Africa (1Y = first-year birds, 2Y = second-year birds, 2Y+ = adults).

	Wing length	Wing length (old outer primaries)	Wing length[1] (new outer primaries)	Bill length	Tarsus length
2Y+	204.4 ± 6.5	203.5 ± 6.2	204.9 ± 6.7	30.1 ± 1.5	48.3 ± 1.7
	(188-226, n = 196)	(194-224, n = 72)	(188-226, n = 124)	(27-33, n = 227)	(42.2-56, *n* = 81)
2Y	199.6 ± 7.9	191.6 ± 4.7	204.6 ± 4.8	30.6 ± 1.4	48.3 ± 1.6
	(186-213, n = 31)	(186-197, n = 12)	(196-213, n = 19)	(27-33, n = 56)	(45-53, *n* = 19)
1Y	195.0 ± 5.8	-	197.4 ± 4.7	29.5 ± 1.4	48.5 ± 2.0
	(175-208, n = 69)		(189-208, n = 24)	(26.5-32.3, n = 68)	(45-52.5, *n* = 26)
one-way ANOVA	$F_{2,293}$ = 53.87	$F_{1,82}$ = 39.53	$F_{2,164}$= 14.47	$F_{2,348}$ = 8.47	$F_{2,123}$ = 0.61
	P < 0.0001	P < 0.0001	P < 0.0001	P < 0.0003	NS
S-N-K test	1Y vs 2Y, 2Y+	-	1Y vs 2Y, 2Y+	1Y vs 2Y, 2Y+	
P < 0.05	2Y vs 2Y+			2Y vs 2Y+	

[1] = only 1Y birds caught before 31 January were included.

Table 3. Linear regressions of wing, bill and tarsus lengths on days (1Y = first-year birds, 2Y = second-year birds, 2Y+ = adults).

Dependent variable	*F*	r^2	*P*	Slope coefficient	constant
wing length	0.18	0.002	0.7	-0.01	207.8
(2Y+)[1]	(df = 128)			(SD = 0.03)	(SD = 6.7)
wing length	6.7	0.08	0.01	-0.019	199.6
(1Y-2Y)	(df = 79			(SD = 0.07)	(SD = 2.0)
bill length	0.41	0.0001	0.84	0.0003	30.0
(2Y+)	(df = 226)			(SD = 0.001)	(SD = 0.3)
bill length	15.9	0.11	0.0001	0.004	28.5
(1Y-2Y)	(df = 123)			(SD = 0.001)	(SD = 0.4)
tarsus length	0.14	0.002	0.7	0.001	48.1
(2Y+)	(df = 80)			(SD = 0.003)	(SD = 0.6)
tarsus length	0.54	0.01	0.46	-0.002	49.0
(1Y-2Y)				(SD = 0.003)	(SD = 1.0)

[1] = adults after post-breeding primary moult

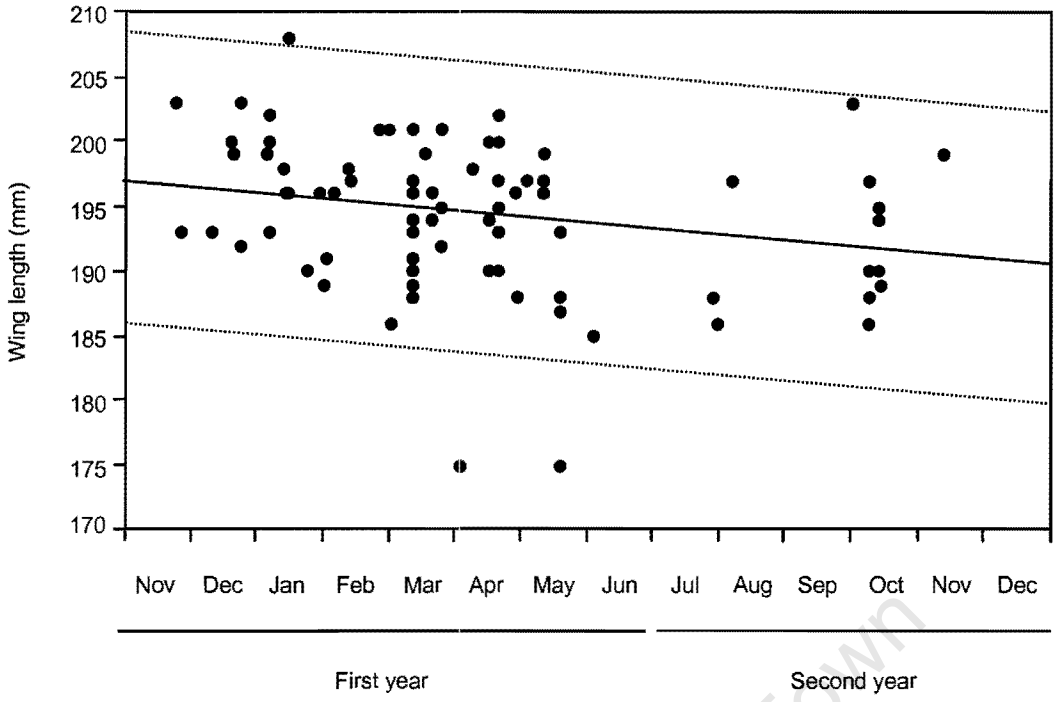

Fig. 2. Seasonal distribution of wing length of first- and second-year birds. First-year birds become second-year birds on 1 July. Solid line represents linear regression, dashed lines are 95% confidence limits (see Table 3).

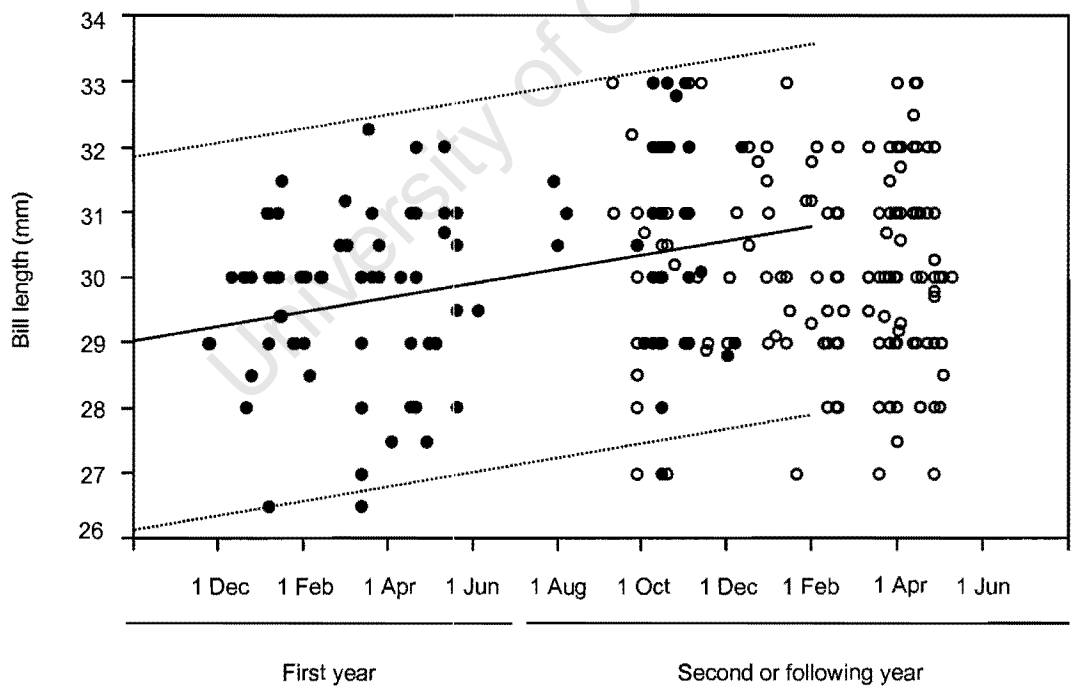

Fig. 3. Seasonal distribution of bill length of first- and second-year birds (solid circles) and adults (open circles). First-year birds become second-year birds on 1 July. Solid line represents linear regression for first- and second-year birds, dashed lines are 95% confidence limits. Adult bill length did not vary throughout the season (see Table 3).

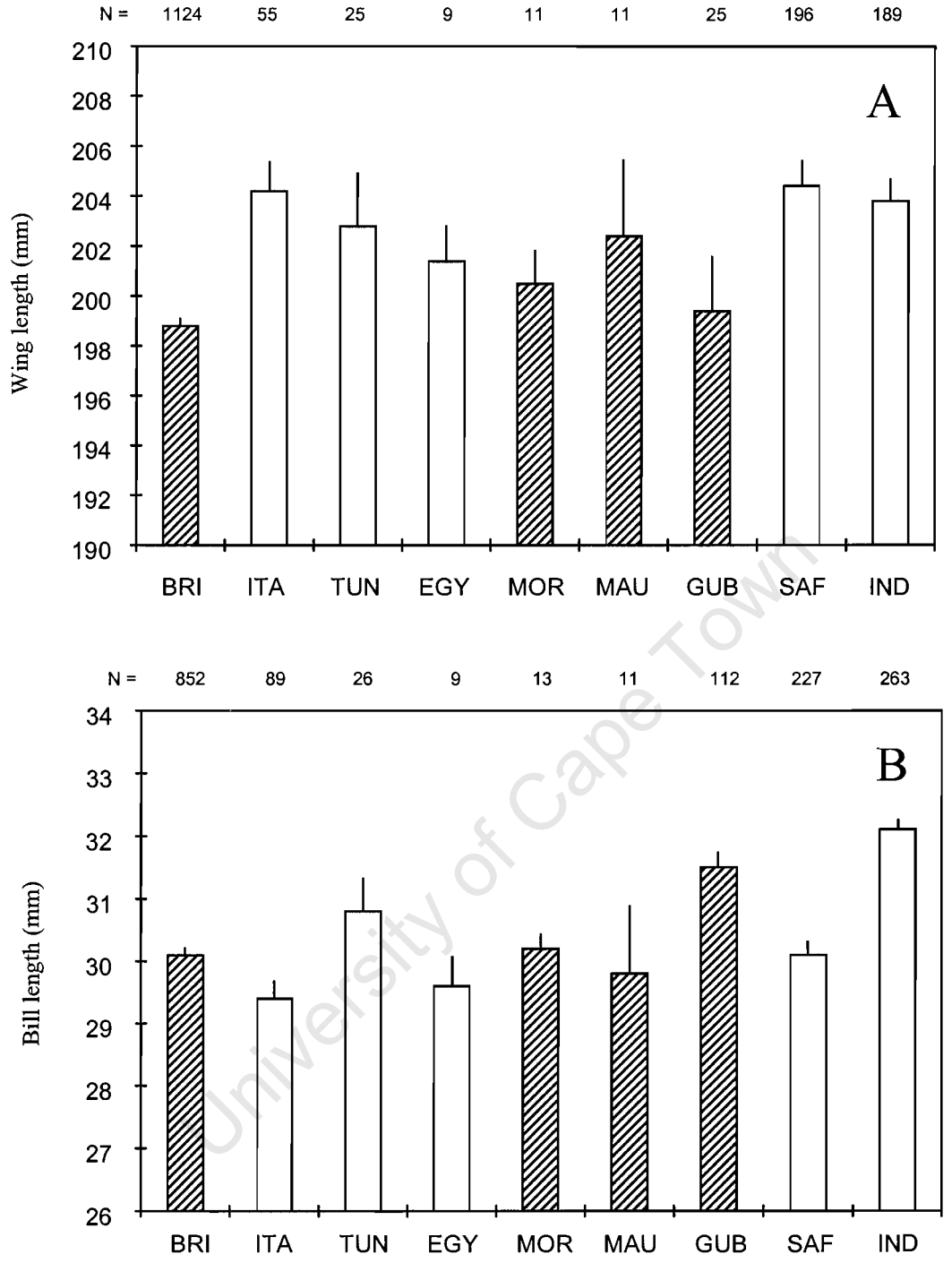

Fig. 4. Wing (A) and bill (B) lengths (mean ± 1.96 SE) of adult Grey Plovers from different areas of the non-breeding range. Hatched bars are countries on the East Atlantic Flyway. BRI = Britain (Branson & Minton 1976), ITA = Italy (Serra & Rusticali 1998), TUN = Tunisia (Zenatello *et al.* 1997), EGY = Egypt (Meininger & Schekkerman 1994), MOR = Morocco (Pienkowski 1972), MAU = Mauritania (Ens *et al.* 1989), GUB = Guinea Bissau (Wymenga *et al.* 1992), SAF = South Africa (this study), IND = India (Balachandran *et al.* 2000). Sample sizes are indicated.

In first- and second-year birds, wing length changed significantly with season, decreasing by 4% in a 12-month period (1 November - 30 October, Fig. 2, Table 3). After the moult of juvenile primaries, wing length of second-year birds did not differ from that of adults (Table 2).

First-year birds had significantly shorter bill lengths than adults (2%) and second-year birds (3.6%); the latter had bills 1.7% longer than adults (Table 2). For first- and second-year birds, bill length increased significantly with season (Fig. 3, Table 3).

There were no significant differences in tarsus length between age-classes (Table 2). In each age class, tarsus length did not vary with season (Table 3).

DISCUSSION

First-year birds were on average significantly smaller than adults in wing length, as in most medium or large-sized waders (Cramp & Simmons 1983) and had a substantial wing length reduction before their first primary moult (4%), due to feather abrasion. Adult wing did not reduce in length probably because of better quality feathers. Tarsus length did not vary among age classes or during the season in first-year birds, indicating that growth and ossification were probably complete before arrival in South Africa. Bill length was shorter in first-year birds and reached mean adult length by June. The same pattern has been observed in Grey Plovers spending the boreal winter in Italy (Serra & Rusticali 1998). As the growth of the bone components of the bill is probably completed at the same time as the development of other skeletal parts, such as tarsus, the slow and late increase of bill length can be attributed to the development of its horny sheath.

It is difficult to find a biological explanation for longer bills of second-year birds in respect to adults. In waders, seasonal changes in bill length have been described for the Sanderling *Calidris alba*. In this species, individuals older than first year showed longer bills between November and January, when moult of forehead feathers could affect the reliability of the measurement (Summers *et al.* 1987b). The same might be valid in our case, with longer-billed birds occurring in September-October, when second-year birds were finishing their first cycle of primary moult (Serra *et al.* 1999) and probably moulting forehead feathers. In most bird species, feathers of the head are usually moulted during last stages of the primary moult, unless body and wing moult are kept separated (Stresemann & Stresemann 1966, Jenni & Winkler 1994). Alternative hypotheses might involve bill length variations due to seasonal changes in diet or foraging tactics (Turpie & Hockey 1996, 1997), with secondary effects on culmen abrasion (Davis 1954) or a variation of the sex-ratio of non-breeding birds. As for other large-sized waders not regularly breeding in their first year, males might migrate northward with a higher frequency than females (the largest sex, see below).

The comparison of average wing lengths of South African Grey Plovers with those given for seven geographical groups distributed along the Palearctic breeding range (museum skins, measurements corrected for shrinkage: Engelmoer & Roselaar 1998) would suggest a breeding origin from Gydan Peninsula eastwards. Populations breeding more to the west seem to have shorter wings (201.2 mm, SD = 2.2, n =8), while more to the east there is an unclear geographical pattern and, at the present state of knowledge, it is difficult to set dividers. From Gydan to Kolyma River, maximum wing length differences between populations were 1.1 mm in males and 3.9 mm in females. Available data from live-trapped breeders confirm that morphometrical differences between Taimyr and Lena Delta populations are small (Hötker 1985, Schekkerman & van Roomen 1995, Exo pers. comm.).

Adults had mean wing lengths 1.2-2.7% longer than birds spending the austral summer at northern latitudes along the East Atlantic Flyway, and 0.2-0.8% longer than those from Tunisia and Italy (Fig. 4a). On average, bill length was 4.7% and 3.3% shorter than in Guinea Bissau and Tunisia, equal to the mean of British birds, and 1.0% and 1.7% longer than in Mauritania and Italy (Fig. 4b). A higher proportion of birds from the westernmost populations in the East Atlantic Flyway might explain the shorter wing lengths observed along that migration routes with respect to the sites of the Central Mediterranean Flyway and South Africa (Fig. 3a). However, the geographical distribution of short- and long-billed populations outside breeding season shows an irregular pattern which cannot readily be linked to the breeding origins and migratory routes suggested above (cf. also Serra 1998, Serra & Rusticali 1998). Significant sexual differences in biometrics have not been detected on museum skins, although females had slightly longer wing, tail, bill, total head, tarsus and tarsus-plus-toe (Cramp & Simmons 1983, Marchant & Higgins 1993, Engelmoer & Roselaar 1998). In contrast, samples of live trapped breeding birds indicated sexual dimorphism. Males were significantly larger than females in western and north-eastern Taimyr (Chylarecki & Sikora 1990, Schekkerman & van Roomen 1995), and females were larger than males in the Lena Delta (Exo pers. comm.). Because a slight sexual size dimorphism does seem to exist, despite the mixed patterns observed, and females probably outnumber males in the southern part of the non-breeding range (Cramp & Simmons 1983, Clancey 1986), it is not possible to further assess the implications of observed differences based on comparison of this mixed-sex average values. An attempt to identify breeding origins of South African Grey Plovers by the application of a POSCON analysis to this dataset gave unrealistic results, suggesting that for this species morphometrical analyses have to be interpreted with caution (Tomkovich & Serra 1999).

Southern African ringing recoveries indicate that some Grey Plovers followed, during southward and northward migrations, a pathway crossing the eastern Mediterranean and the Black Sea (Vandewalle 1988, Underhill 1997). This suggests that Grey Plovers heading to South Africa, once they have reached the Mediterranean/Black Sea Region, may cross the Sahara desert, meet the Atlantic ocean coast and then follow it to their destinations. This path approaches a great-circle route linking southwestern Africa to central Siberia and has also been suggested for the South African populations of Curlew Sandpipers *Calidris ferruginea* (Elliott *et al.* 1976, Wilson *et al.* 1980), Sanderlings (Summers *et al.* 1987b) and Turnstones *Arenaria interpres* (Summers *et al.* 1989). Migration across the Sahara was suggested by studies of initial directions taken by Grey Plovers leaving Ghana in spring (Grimes 1974, Grimes & Vanderstichelen 1974) and several inland observations (Salvan 1968, Wells & Walsh 1969). For the northward migration, there is evidence of migratory movements of Grey Plovers along the coast of the eastern Atlantic (Underhill 1989).

There is no direct evidence of Grey Plovers reaching South Africa along the Western Asian Flyway. This is, however, strongly suggested by their the presence along the eastern coast of Africa (Underhill 1997) and passage across the interior of Africa, where birds rest at inland waterbodies (see, for South Africa, Prozesky & Campbell 1951, Liversidge 1958, Milstein 1975, Skead & Dean 1977, Dowsett 1980, Underhill 1997). As for other arctic waders, South Africa appears to be the terminal point of at least two flyways (Summers *et al.* 1987a,b, Harrison *et al.* 1997).

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CHAPTER 6

BIOMETRICS, MOULT AND MIGRATION OF GREY PLOVERS *PLUVIALIS SQUATAROLA* AT MIDA CREEK, KENYA

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Ringing data on 269 Grey Plovers Pluvialis squatarola *caught between 1977 and 1988 were analysed. Adult started primary moult soon after arrival in August and September. Mean starting date of adult primary moult was estimated on 13 September, primary moult duration as 130 days. First-year birds had not started primary moult by early May. Body mass of adults in primary moult was stable from September to February, averaging 205 g, but increased at the end of the moult, in March and April. Pre-migratory body mass was estimated at 268 g and would allow a non-stop flight as far as the south-eastern Mediterranean or the northern Persian Gulf. Mean wing length increased in March and April, possibly due to the arrival of longer-winged migrants from southern Africa or an earlier departure of males. A decrease in numbers was observed from the second half of April and by mid-May all adults had left the area. In June-July, the number of first-year birds was c. 25% of the total summer population.*

INTRODUCTION

The Grey Plover *Pluvialis squatarola* is a Palearctic migrant to the coasts of Kenya, common on creeks, estuaries and coral flats between August and April. Some first-year birds remain throughout the year (Fogden 1963, Milligan 1979, Zimmerman *et al.* 1996). From available counts, irregularly scattered over a 20-year period, the total population wintering on the Kenya coast was estimated at *c.* 5 000 birds (Britton & Britton 1976, Bryant 1980, Pearson 1984, Pearson & Britton 1980, Seys *et al.* 1995, Summers *et al.* 1987). Except for a few on the shores of Lake Turkana (Pearson *et al.* 1992), wintering Grey Plovers are rare in inland Kenya (Lewis & Pomeroy 1989).

A decade of wader ringing at Mida Creek, one of the most important wader roosts on the Kenya coast, has provided data from which biometrics, seasonal body mass variations and moult patterns can be described. This paper aims at shedding some light on Grey Plovers spending the non-breeding period at tropical latitudes and at identifying their possible migration strategies and routes.

STUDY AREA AND METHODS

Between 1977 and 1988, Grey Plovers were caught with mist-nets and ringed, together with other waders, at Mida Creek (3°20'S, 39°55'E), Kenya. Ringing activities were carried out between August and May. Eight to ten 20 m nets were used at night on tidal sand-flats on the north-west edge of the creek. These were sited 50-100 m from and mostly at right angle to the mangrove shoreline in an area where waders tended to congregate on the rising tide, but tended to remain over high tide only on low neaps (less than 2.4 m). Catching was carried

out on neap periods with tides of 2.3-2.6 m, on the rising tide (between 20.00 and midnight) and usually on the falling tide as well (01.00-05.00 hours).

Birds were aged according to plumage characters (Prater et al. 1979, Cramp & Simmons 1983) and primary moult stage (cf. Serra et al. 1999) and divided into the following categories: first-years (birds in the first year of life, from arrival in October to 30 June of the following year), second-years (from 1 July of their second calendar year to the end of the first complete moult in September-November of the same year), birds older than second year (from arrival in August to the end the primary moult) and adults (birds older than first-years, i.e. all birds after primary moult completion).

Wing length was measured to the nearest 1 mm, bill length from tip to feathering also to the nearest 1 mm; body mass was recorded with spring balances to the nearest 1 g. No correction indices for body mass loss were applied because the time gap between capture and ringing was not recorded. However, birds were usually weighed within one hour from capture.

Moult scores of individual primary feathers were recorded in the field according to Snow (1967) and then converted to percentage feather mass grown (Underhill & Joubert 1995). Moult parameters were estimated by the statistical method of Underhill & Zucchini (1988); an unpublished version of the model, which allows data to be both of types 1 and 2, was applied. This latter version considers both birds with full details of primary moult (data-type 2) and those for which only the information that they were moulting is available (data-type 1) (Underhill & Zucchini in litt.). Three adults which were still in active moult in March and April and had low body mass values were excluded from calculations of primary moult parameters. We assumed that they were second-year birds which were not going to migrate. The percentage of breeding plumage was recorded using the following categories: 0%, 1-30%, 31-60%, 61-90%, 91-100%. For seasonal analyses, dates were converted into days and numbered from 1 July to 30 June. For second-year birds, day numeration was made additive, i.e. started from 1 July of the previous year. Grey Plovers were occasionally counted between 1976 and 1988 in the diurnal tidal roosts and notes on age-class composition, percentage of birds in active primary moult and breeding plumage were taken.

RESULTS

Two-hundred and seventeen adults were caught between September and April, 42 first-year birds between October and May and 10 second-year birds between August and October. No ringing recoveries have been made of these birds.

After completion of primary moult, the mean wing length of adults did not change between December and February (ANOVA, $F_{2,14} = 0.37$, $P = 0.7$), but increased by about 2% in March and April (ANOVA, $F_{1,57} = 11.9$, $P = 0.001$) (Table 1). Mean wing length did not differ before and after primary moult, when birds older than second years with old outer primaries were compared with adults with new outers (ANOVA, $F_{1,84} = 0.25$, $P = 0.6$). Adults had 1% longer wing than first-year birds (ANOVA, $F_{1,56} = 1.54$, $P = 0.2$). Bill length did not significantly vary among age classes (ANOVA, $F_{2,87} = 0.69$, $P = 0.5$), but adults had bills 1% longer than first-year birds (Table 1).

Table 1. Wing and bill length (mm) of Grey Plovers caught at Mida Creek, Kenya. Mean (standard deviation), range, sample size are given.

	Adults	Second years	First years
Old primaries[1]	201.1 (5.3) 189-211, 69	199.2 (5.0) 193-207, 5	-
New primaries[2]	201.8 (4.6) 197-213, 17	-	199.9 (5.6) 188-212, 41
New primaries March-April	206.3 (4.5) 194-217, 42	-	-
Bill	31.1 (1.3) 27-33, 72	31.0 (1.9) 28-33, 5	30.7 (1.0) 30-33, 13

[1] = Birds older than second year caught in September-January with 10th primary not replaced and active primary moult.
2 = Period limited to December-February for adults with 10th primary replaced and October-January for first years

Adult primary moult duration was estimated as 130 days (SD = 4), with mean starting date 13 September (SD = 2), mean completion date 19 January (SD = 3) and standard deviation 25 days (SD = 2) (Fig. 1). First-year birds had not started primary moult by early May; all second-year birds caught in August-October were moulting juvenile primaries (primary score range: 14-49, n = 10). Most adult Grey Plovers arrive back on the Kenya coast with old primaries, but moult evidently starts soon after arrival. Out of 420 adults counted on 14 September 1975 in the Mida roost, 50% had commenced primary moult; this information, which is of data-type 1, was included in the model. No birds with two active primary moult cycles were observed, but only a few second-year birds were examined.

The mean body mass of adults in moult was stable from September to February, averaging 205 g (SD = 14.9, range = 171-250 , n = 118; ANOVA, $F_{5,112} = 1.89$, $P = 0.1$). Pre-migratory mass increase started in March-April and was limited to birds which had finished primary moult (Fig. 2). The mean value for the last half of March and April mass distribution was 268 g (SD = 12, range 250-287, n = 17). This may be taken as an estimate of the average mass of birds ready to take off (see Zwarts et al. 1990).The mass of first- and second-year birds showed no clear seasonal changes (ANOVA, $F_{10,41} = 0.79$, $P = 0.6$) (Fig. 3.).

The extent of breeding plumage was recorded on only a minority of the adults caught throughout the seasons (Fig. 4). Birds arrived in autumn at various stages of breeding plumage. Diurnal observations on roosting flocks confirmed that most adults had over 30% breeding plumage in early September, some with all-black underparts. Many retained traces of breeding plumage until late October or even November. New breeding plumage began to appear in some of the birds with completed primary moult as early as February; it was common and often more than 30% of the birds had some breeding plumage by late March. In April, most birds had partial breeding plumage (usually 30-90%) but only 9% of those caught were fully moulted.

In June-July, there were only first-year birds at Mida and numbers were about a quarter those in winter (Fig. 5). Adults began to arrive in early and mid-August and reached peak numbers by mid-September. The main arrival period was thus between late August and mid-September. First-year birds were caught from October. There was no marked decrease in the flock size up to early April. Numbers decreased during the second half of April, and the remaining adults left rapidly between about 25 April and 5 May.

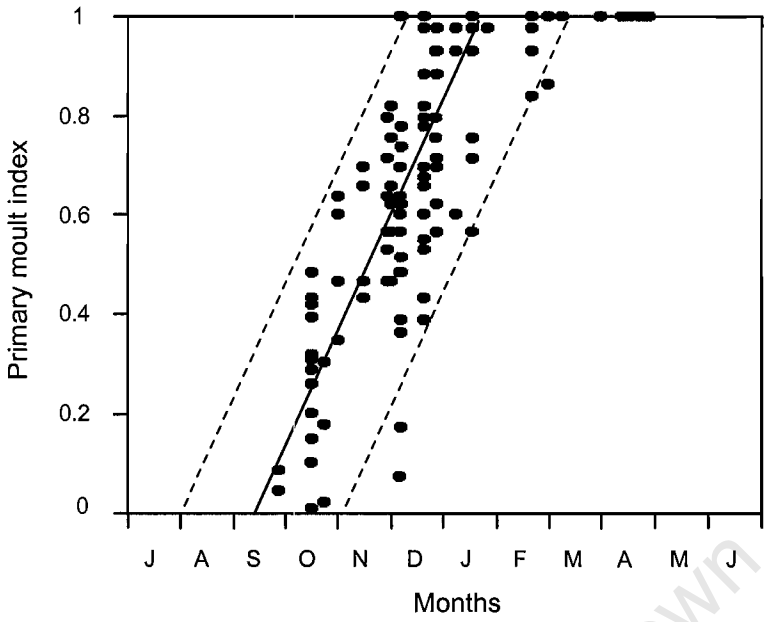

Fig. 1. Seasonal distribution of primary moult indices of adult Grey Plovers *Pluvialis squatarola* in Kenya. The solid line is the average progression of the moult; the dashed lines include *c.* 95% of the population.

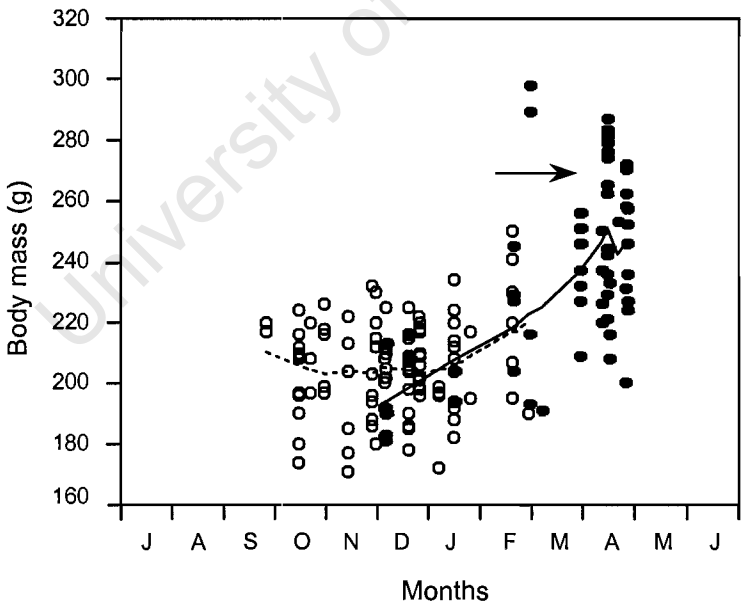

Fig. 2. Seasonal body mass variation of adult Grey Plovers *Pluvialis squatarola* in Kenya. Open dots are birds in active primary moult, solid dots are birds after moult. Lines are lowess regressions fitted to 50% of the points. Dashed line fitted to birds in moult, and solid line to birds with completed moult. The arrow indicates the estimated average value of birds after mid-May and probably ready to take off (268 g).

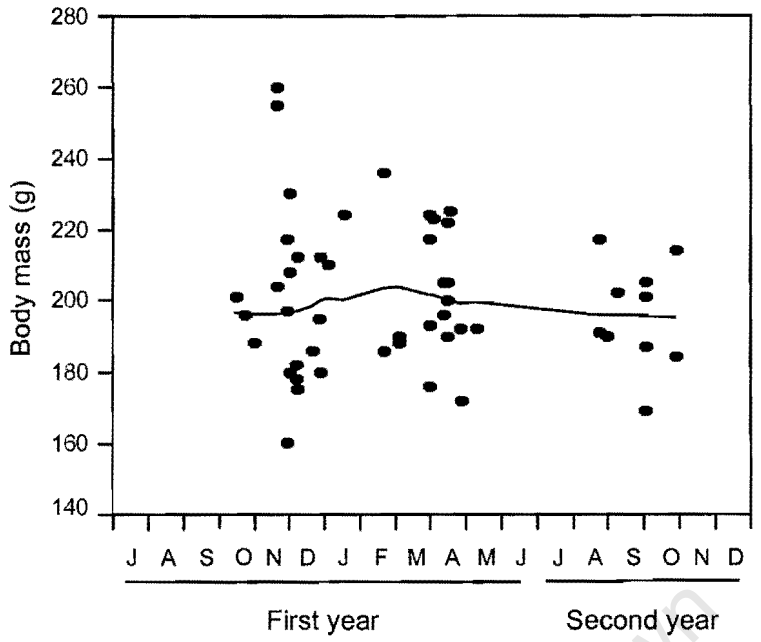

Fig. 3. Body mass variation of first/second years Grey Plovers *Pluvialis squatarola* in Kenya. The line is a lowess regression fitted to 50% of the points.

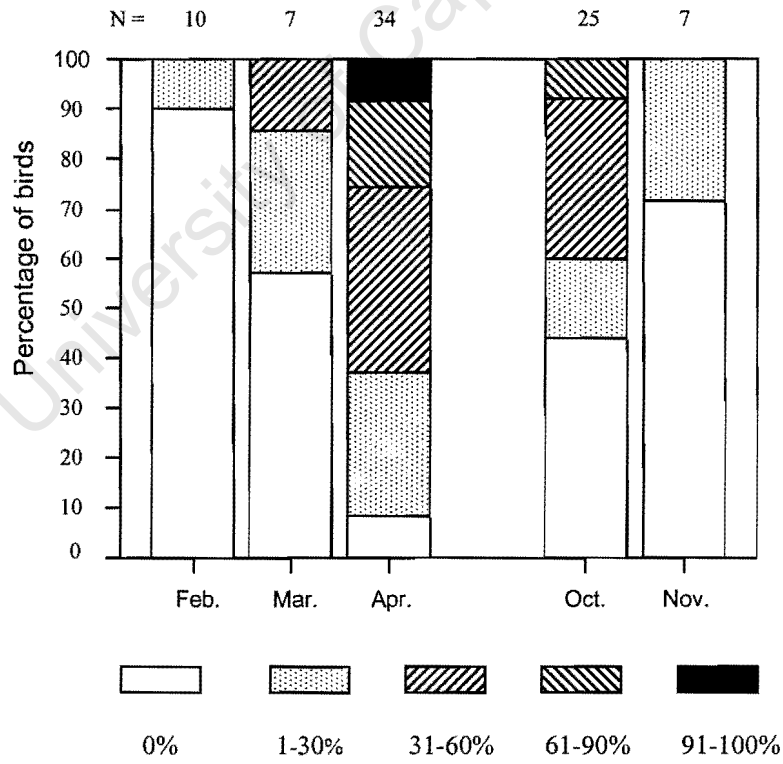

Fig. 4. Monthly distribution of breeding plumage of adult Grey Plovers *Pluvialis squatarola* in Kenya.

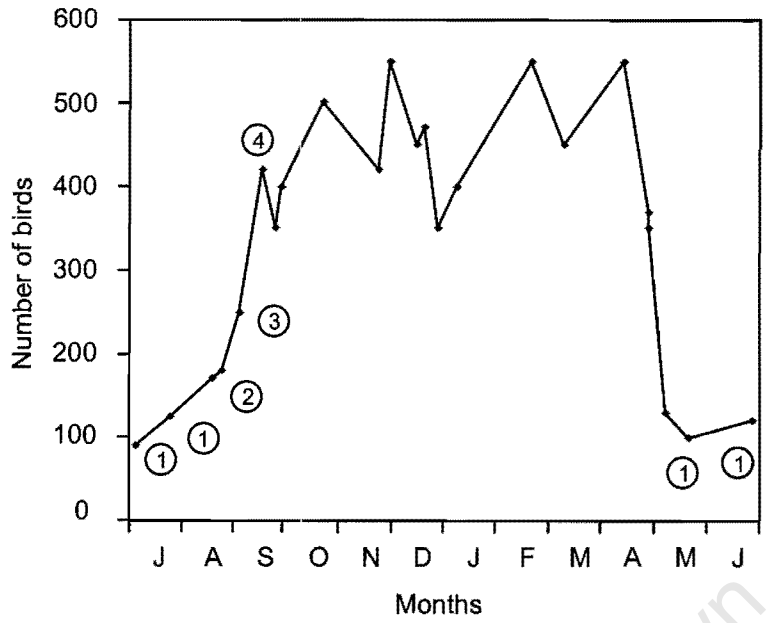

Fig. 5. Numbers of Grey Plovers counted in the Mida tidal roost between 1976 and 1988. 1 = all first-year birds; 2 = < 5% adults; 3 = 70% adults; 4 = most adults, c. 50% with unmoulted inner primaries.

Discussion

Morphometric analyses did not allow the identification of the breeding origins of Kenyan Grey Plovers, because samples available from the Siberian breeding grounds are small and morphometric variations are slight and often controversial (Byrkjedal & Thompson 1998, Engelmoer & Roselaar 1998, Tomkovich & Serra 1999). Furthermore, wing and bill length variations from southern African to European wintering sites are not clear and the maximum observed differences amounted to only 3% and 6% respectively (Serra & Rusticali 1998, Serra *et al.* 2001). Moreover, morphometrically different breeding populations can intermingle at wintering sites, and there is probably a sexual segregation in the geographical distribution, with the larger-sized females more abundant at southern latitudes than males (Cramp & Simmons 1983). Out of 15 specimens from Durban Bay, South Africa, 86.6% were females and 13.3% males (Clancey 1986). The size of character variations is so small that systematic biases in measurements might well account for most of these differences. Primary abrasion, inclusion of birds with the longest primary still growing and inter-observer variability are the most important sources of biases or errors.

The increase in wing length in March and April might be explained by the arrival of migrants from southern latitudes. South Africa holds the longest-winged populations of the continent and some of these migrate northward along the coast of the Indian ocean (Serra *et al.* 2001). The time of arrival of longer-winged birds in Kenya fits with departures from South Africa, where birds are ready to migrate from mid-March onwards (Serra *et al.* 1999). A second hypothesis is that males, which are the shorter-winged sex, leave Kenya before females. The difference in wing length between sexes, 1.3% in British Grey Plovers (Serra in prep.), might therefore explain the 2% variation observed in Kenya. The absence of lean birds during the fattening period, together with the pattern of seasonal fluctuation of Grey Plover numbers, further suggest that the arrival of migrants from the South, if any, is negligible.

Feather wear caused a small decrease (0.4%) in wing length of adults in Kenya and variations of the same size (0.5-0.7%) were found at other sites where Grey Plovers have a primary moult duration of 120-130 days. By contrast, larger reduction rates of 1.0-3.0% have been noted at sites where moult duration is c. 90 days. This suggests that durability of primary feathers is related to moult duration (Serra in press). The mean body mass of wintering adults was 4% lower in Kenya than in South Africa during the same period (214 g, Serra et al. 1999) but 5% higher than in Guinea Bissau (196 g, Ruiters & Fokker 1998). This accords with the general observation that waders wintering in tropical latitudes are leaner than those wintering at either northern or southern sites, where environmental conditions are less predictable (Barter 1987, Pearson 1987, Barter et al. 1988, Minton & Serra 2001).

Grey Plovers embarking on migration from Kenya had an estimated mean body mass some 13% lower than that of birds leaving South Africa (268 g vs. 310 g, Serra et al. 1999), suggesting that Kenyan birds covered shorter distances en route to their next refuelling area. A similar percentage difference in departure body mass was observed between South Africa and Kenya for Little Stints Calidris minuta and female Ruffs (Middlemiss 1961, Pearson 1981, 1987, Summers & Waltner 1978). The energy load of 60-70 g observed in Kenya would allow Grey Plovers to cover a distance of 3 600-4 100 km (Pennycuick 1989). This means that they could fly non-stop as far as the south-eastern Mediterranean (Nile Delta) or the northern Persian Gulf on a direct route. Three major potential refuelling areas can be identified to the N and NNE of Kenya, on flyways to East Europe and West Asia:

1. The Gulf of Aden;
2. The Persian Gulf;
3. The Azov/Black Sea and the Caspian Sea.

The extensive mudflats of the Gulf of Aden, along the coasts of Djibouti, NW Somalia and S Yemen, some 1 500-1 800 km NNE from Mida Creek, are a key site for wader refuelling along the West Asian Flyway (Summers et al. 1987), but they might be leapfrogged by most Kenyan Grey Plovers on northward migration. Direct flights to the Azov/Black Sea or the Caspian Sea would require a fat load of about 100 g and seem precluded for most individuals. The Persian Gulf area may therefore be the main destination for birds leaving southern Kenya (Zwarts et al. 1991).

South African Grey Plovers have on average a fat and protein load of 100 g (Serra et al. 1999) and can therefore fly uninterruptedly for c. 5 400 km. A migratory route following the coastline from Langebaan Lagoon in the Western Cape, South Africa, to Mida Creek is c. 5 200 km long and fits well with the estimated distance. The same flight across the interior is c. 4 100 km.

The extent of breeding plumage in April, when migrants from southern Africa were apparently present at the study area, varied from none at all to complete breeding plumage, in line with the high variation also observed in Australia, Guinea Bissau, Mauritania and South Africa (Minton & Serra 2001, Ruiters & Fokker 1998, Serra et al. 1999, Zwarts et al. 1990). Given the fact that females are prevalent in the southern part of the non-breeding range (Cramp & Simmons 1983, Clancey 1986), the high proportion of birds which depart with little or no breeding plumage might be explained either as a consequence of the short period available for body moult between the end of the primary moult and the onset of northward migration (Serra et al. 1999) or as a character of females. If time limitation is an important factor, the less complete breeding plumage of females on the breeding grounds might be partly a consequence of their more tightly scheduled annual activities, due to

longer migration journeys. Studies on the effects of proximal factors on moult and the development of breeding plumages would probably reveal unexpected patterns.

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CHAPTER 7

BIOMETRICS AND MOULT OF GREY PLOVERS *PLUVIALIS SQUATAROLA* IN AUSTRALIA

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Data on 299 Grey Plovers Pluvialis squatarola *banded in northwestern Australia (NWA) and in Victoria, southeastern Australia (SEA) in 1980-1999 were analysed. Sightings of birds leg-flagged in SEA indicated refuelling sites in Japan on both northward and southward migration. A POSCON discriminant analysis on biometrical data suggested that Grey Plovers caught in Australia originated from populations breeding in Siberia east of the Lena River and that the discrete population of Wrangel Island was better represented in SEA. In NWA, departures to the breeding grounds occurred mainly in April, with an average departure body mass of 311 g. This would allow a non-stop flight of c. 4200-5400 km, enough to reach the coasts of northern Vietnam or China. Primary moult duration and mean starting date were 128 days and 5 October in SEA, and 121 days and 10 September in NWA. Grey Plovers departed northwards with little or no breeding plumage.*

INTRODUCTION

The Grey Plover *Pluvialis squatarola* has a circumpolar breeding distribution and migrates to the milder regions of the northern hemisphere and throughout the southern hemisphere for the non-breeding season. In Australia it is a coastal species, mainly distributed along the northern and southeastern coasts, where it concentrates at few sites (Marchant & Higgins 1993). Seventeen sites hold over 90% of the Australian population which is estimated at *c.* 12 000 birds, i.e. 75% of the East Asian/Australasian Flyway Population (Watkins 1993). It therefore seems that only a minority of the birds belonging to this flyway spends the austral summer in south-east Asia. However, China, Japan, Korea and other parts of Asia will obviously play an important role during the biannual migratory movements from the Arctic breeding grounds.

This paper summarises the results of banding activities carried out in Australia during the last 20 years, focusing on biometrics, breeding origins and moult patterns. Migration strategies and movements are also considered.

STUDY AREA AND METHODS

Grey Plovers were caught in cannon-nets (mostly) and mist-nets in Victoria (coordinates: 38-39°S, 144-147°E), southeastern Australia (SEA), and in the Broome-Port-Hedland area (coordinates: 18-20°N, 119-122°E), northwestern Australia (NWA).

Birds were aged according to plumage features and primary moult state (Prater *et al.* 1976, Marchant & Higgins 1993). Each bird was assigned to one of three age categories: first-year, second-year, older than second-year and adult. The last included second-years after their first complete moult. The

following measurements were taken: wing length (flattened chord) to the nearest 1 mm, exposed culmen and total head lengths to the nearest 0.1 mm. Body mass was recorded with spring balances to the nearest 1 g. In addition to the metal ring, birds were marked with leg-flags identifying the catching site (orange = SEA; yellow = NWA).

Primary moult was recorded according to Ginn & Melville (1983): old feathers were scored 0, new feathers 5 and growing feathers from 1 to 4 in relation to their stage of growth. Feather scores were then transformed into percentage feather mass grown and a moult index was calculated for each bird (Underhill & Summers 1993). Moult timing, duration and speed were obtained applying the model developed by Underhill & Zucchini (1988) and Underhill *et al.* (1990). We assumed that data from SEA were, on each date, a random sample of the following moult categories: not yet started, in moult, completed, and therefore fulfilled the conditions of data-type 2 of the above mentioned model. Data from NWA were assumed to be random samples of birds which had not yet started moult and in moult, because of a two-month gap in sampling period at the end of the moult (January and February). These data were therefore analysed as data-type 5 (Underhill *et al.* 1990). The percentage of breeding plumage was recorded.

The breeding origins of Australian Grey Plovers were predicted by means of a POSCON discriminant analysis (Engelmoer & Roselaar 1998, van der Sluis *et al.* 1991). This technique assigns each bird a typicality probability, which represents the 'degree of resemblance' of an individual to the groups used as reference samples. The following reference groups were considered: (1) West Siberia, birds originating from Yamal to Taimyr, (2) East Palearctic/North Alaska, birds from Siberia east of the River Lena and West Alaska, (3) Wrangel Island (Table 1, Engelmoer & Roselaar 1998). The analysis was based on two measurements, wing and culmen lengths.

Table 1. Measurements of wing and bill lengths of three Grey Plover breeding populations (Engelmoer & Roselaar 1998) used as reference samples for identifying the origins of Australian Grey Plovers. Mean, (standard deviation), sample size given.

	Yamal & Taimyr	E Siberia & Alaska	Wrangel Island
Wing length	205.5, (4.0)	206.1, (5.6)	210.4, (5.0)
	n = 47	n = 48	n = 29
Bill length	28.9, (1.3)	30.9, (1.3)	29.3, (1.7)
	n = 45	n = 48	n = 29

RESULTS

In 1980-1999, 100 Grey Plovers were ringed in SEA (five first-years, six second-years and 89 adults) and 199 in NWA (20 first-years, 14 second-years, 162 adults and three unaged birds). The proportion of first-year birds in catches (8.4%) seems low but it is typical of most medium/large waders in Australia (Australian Wader Study Group/Victorian Wader Study Group, unpubl. data).

Table 2. Morphometrics of Grey Plovers ringed in Victoria (SEA) and in the Broome-Port-Hedland area (NWA) in 1980-1999. Mean, (standard deviation), range, sample size given; means in mm are compared by t-tests. There was no significant difference in bill length between adults in active post-breeding moult and those after moult.

Adults

	SEA	NWA	t-test
Wing	207.8 (4.8)	205.6 (4.9)	$t_{237} = 3.43$
	197-220, 93	186-218, 146	P = 0.001
Wing	208.9 (3.7)	206.0 (4.6)	$t_{113} = 2.3$
(new primaries)	202-216, 15	195-218, 99	P = 0.02
Wing	207.8 (4.9)	204.8 (5.4)	$t_{120} = 3.14$
(old primaries)	197-220, 76	186-217, 47	P = 0.02
Head+bill	70.1 (2.0)	70.1 (1.9)	$t_{241} = 0.23$
	65.8-79.3, 89	65.4-79.6, 154	NS
culmen	31.1 (1.5)	32.6 (1.4)	$t_{229} = 7.42$
	28.6-35.7, 75	28.8-37.3, 156	P < 0.001

Second-years

	SEA	NWA	t-test
Wing	198.3 (8.9)	206 (5.8)	$t_{14} = 1.6$
	184-210, 12	201-212, 4	NS
Wing	208	-	-
(new primaries)	1		
Wing	198 (9.0)	206 (5.8)	$t_{12} = 0.1$
(old primaries)	184-210, 10	201-212, 4	NS
Head+bill	70.2 (1.5)	69.8 (1.0)	$t_{17} = 0.6$
	68-73.1, 14	68.6-71, 5	NS
culmen	33.1 (1.5)	31.3 (0.5)	$t_{12} = 2.4$
	30.1-35.4, 10	30.8-31.7, 4	P < 0.04

First-years

	SEA	NWA	t-test
Wing	200.0 (1.6)	198.4 (6.7)	$t_{22} = 0.52$
	189-202, 5	189-213, 19	NS
Head+bill	71.4	70.0 (2.5)	-
	1	66.9-76.8, 19	
culmen	31.7 (0.58)	32.9 (1.2)	$t_{21} = 1.82$
	31.0-32.0, 3	30.3-34.8, 20	NS

In SEA, six adults were recaptured in following seasons, the oldest one being after five years and 344 days. In NWA, four adults were locally retrapped in seasons following that of ringing, the longest elapsed period being nine years and 241 days. No foreign ringed birds were caught in Australia, and no Australian-marked birds were retrapped abroad. However, at least five birds (involving eight sightings) marked with leg-flags on 18 October1997 in SEA (N.W. Swan Bay: 38°13'S, 144°39'E) were observed between 8 and 18 August 1998 in the Tokyo Bay area (35°40'N, 140°E).

Table 3. Monthly body masses of Grey Plovers ringed in Victoria (SEA) and in the Broome-Port-Hedland area (NWA) in 1980-1999. Mean (g), (standard deviation), range, sample size given.

	Adults		Second-years		First-years	
	SEA	NWA	SEA	NWA	SEA	NWA
July	-	-	-	-	-	208 n = 1
August	-	178.3 (11.7) 165-187, n = 3	-	-		
September	230 n = 1	211.9 (13.2) 188-240, n = 32	267 n = 1	210.9 (15.9) 182-228, n = 10	-	-
October	222.6 (16.7) 180-255, n = 59	214.5 (19.2) 185-240, n = 13	228.8 (25.9) 210-265, n = 4	222 (10.6) 214-234, n = 3	-	-
November	243.1 (10.4) 224-260, n = 17	206 n = 1	243 n = 1	-	-	-
December	-	229.6 (11.3) 205-245, n = 14	-	-		
January	225 n = 1	-	-	-	-	-
February	307.3 (20.1) 270-330, n = 13	-	-	-	255 (n = 1)	-
March	380.0 (14.7) 365-395, n = 4	292.1 (20.6) 235-330, n = 42	-	-	-	204.7 (25.1) (n = 4, 173-300)
April	310 (n = 1)	277.4 (30.8) 206-370, n = 61	-	-	265.0 (7.1) 260-270, n = 2	211.5 (36.7) 173-300, n = 15
June	-	-	-	-	226.0 (22.6) 210-242, n = 2	-

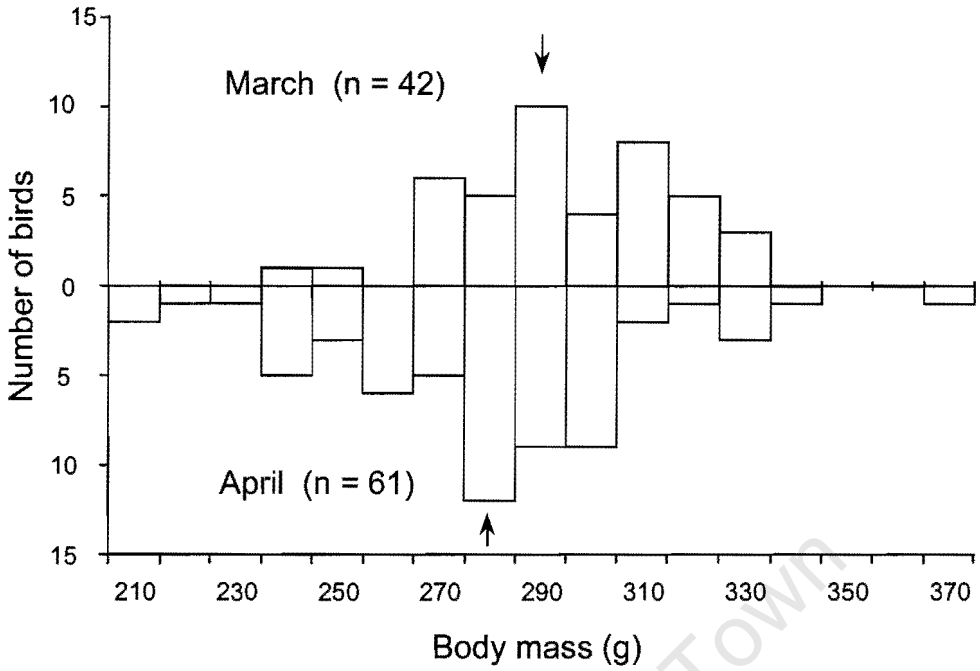

Fig. 1. Body mass frequency distribution of adult Grey Plovers *Pluvialis squatarola* trapped in March and April in the Broome-Port-Hedland area, NWA. Arrows indicate the respective mean values.

Four more individuals were observed in the same area between 22 April and 20 May 1999. Another bird was seen at a different location near Tokyo on 12 August 1998. A bird flagged in NWA was observed at Kanghwa Island, South Korea (37°34'N, 126°23'E) on 15 May 1999.

Adults were mainly caught in October-November (79%) and February-March (18%) in SEA, and in September-December (36%) and March-April (62%) in NWA.

Biometrics and breeding origins

Adults from SEA had wings 2 mm (1%) longer than adults from NWA (Table 2). This difference was still evident when birds with old or new primaries (i.e. birds before shedding P10 or with full grown P10) were selected. In each area, there were no significant differences in wing length between birds with old and new primaries (t-tests) and feather reduction due to wear was *c.* 1 mm (0.5%).

Adult bill length was 1.5 mm (5%) shorter in SEA than in NWA, while total head length did not vary between the two areas (Table 2). Adult bill length did not significantly vary within each area when birds in active post-breeding moult and birds after moult were considered (t-tests).

Between-site comparisons in second and first-year birds were not significant (except culmen length in second-years) but sample sizes were small (Table 2).

The application of a POSCON analysis for assessing breeding origins of adults trapped in SEA estimated the following composition: 60% of birds originated from the East Palearctic/North Alaska population, 39% from Wrangel Island and 1% from West Siberia. The estimate for NWA birds was: 94% from East Palearctic/North Alaska, 4% from Wrangel Island and 2% from West Siberia.

Average body masses of adults showed a marked seasonal pattern in both areas: low values in September-December and high values in February-April (Table 3). In the former period, mean body mass of

adults in SEA was 6% greater than in NWA (227.3, SD = 17.6, n = 77 vs. 214.7, SD = 17.6, n = 63; $t_{138} = 4.2$, P < 0.0001). In NWA, adults trapped in March had greater mean body mass than those captured in April ($t_{101} = 2.71$, P = 0.008) and showed different frequency distributions (Fig. 1). March birds had a negatively skewed distribution (Sk. = - 0.368, SE = 0.365), April birds a positive one (Sk. = 0.076, SE = 0.306). Taking the average body mass of the upper half distribution of March-April adults as the threshold value for identifying birds ready to start migration (Zwarts *et al.* 1990), an average take off value of 311 g is suggested for NWA birds. Although the SEA March/April sample was small (five birds), data suggested greater take off body masses, averaging *c.* 380 g.

Body mass of second-year birds was not compared to that of adults due to small sample sizes. First-years were on average lighter than adults and did not reach pre-migratory values (Table 3).

Primary moult

In NWA, mean starting date of primary moult was 10 September (SD = 2 days), mean completion date 9 January (SD = 4 days), mean duration 121 days (SD = 5 days), standard deviation parameter 12 (SD = 1). In SEA, mean starting date was 5 October (SD = 3 days), mean completion date 9 February (SD = 5 days), mean duration 128 days (SD = 6 days), standard deviation parameter 16 days (SD = 1). The first bird in active moult was observed on 2 September in NWA and on 1 October in SEA (Fig. 2).

There was no evidence of adults arriving in suspended moult, after having carried out the moult of inner primaries on the breeding grounds or at an earlier stopover site on migration, as recorded along the East Atlantic Flyway (cf. Serra 1999). However, some other plovers in the East Asian/Australasian Flyway, notably the Greater Sandplover *Charadrius leschenaultii* and the Oriental Plover *Charadrius veredus*, do exhibit this moult behaviour (CDTM, pers. obs.).

Plumage

In October, SEA adults had more breeding plumage than NWA in September; in March and April, NWA adults had only small fractions of the breeding plumage (Fig. 3). Visible migratory departure observations confirm that Grey Plovers leave Australia before acquiring much of their breeding plumage, in contrast to most other species (CDTM, pers. obs.).

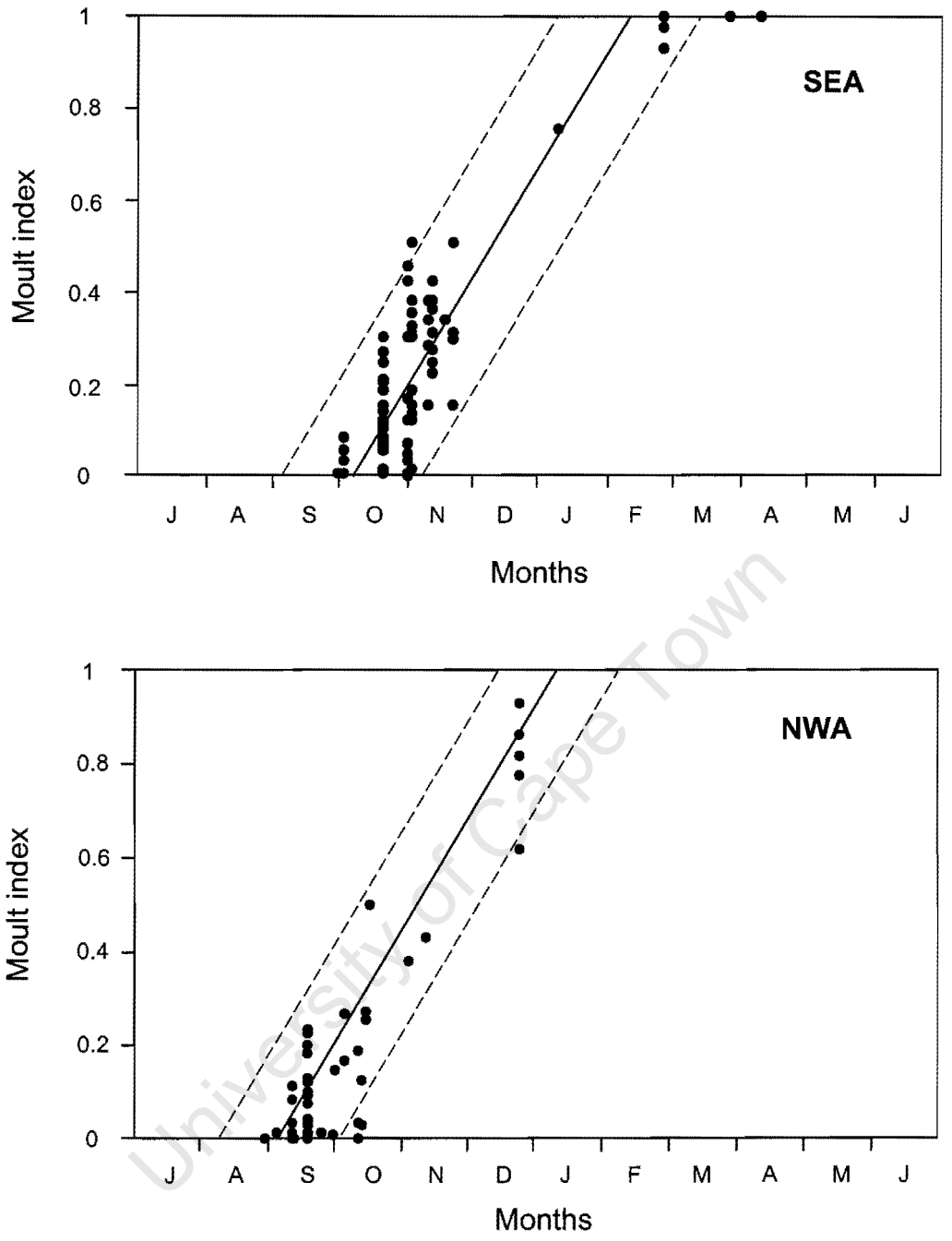

Fig. 2. Timing of primary moult for adult Grey Plovers *Pluvialis squatarola* in the Broome-Port-Hedland area (NWA) and in Victoria (SEA). Moult index was expressed as percentage of feather mass grown. Dashed lines enclose approximately 95% of the population, solid line estimates average moult progression.

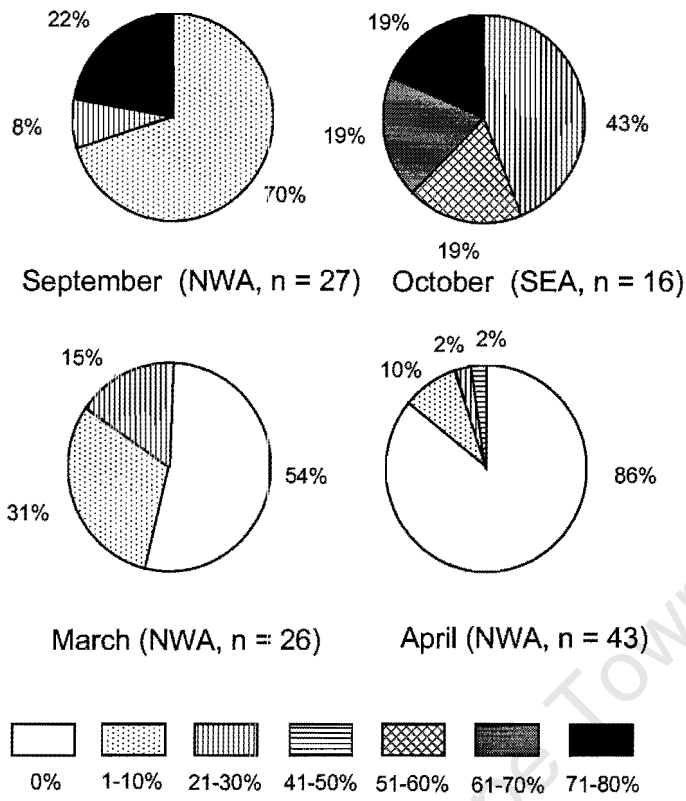

Fig. 3. Percentages of breeding plumage of adult Grey Plovers *Pluvialis squatarola* trapped in the Broome-Port-Hedland area (NWA) and in Victoria (SEA). September and October samples have only birds older than second-year.

DISCUSSION

SEA and NWA Grey Plovers were morphometrically distinct in wing and culmen lengths. This suggests that at least two populations or different assemblages of mixed populations occur. The difference in culmen length cannot be related to measurement biases originating from different seasonal feathering or moult conditions at the base of the bill (cf. Summers *et al.* 1987, Barter 1987, 1992, Serra *et al.* 1999), because culmen length did not vary within each area when birds in and after active moult were compared. The non-significant difference in total head length should therefore indicate that longer-billed birds had shorter heads and *vice-versa*. No significant sexual differences in biometrics have been detected either in living birds (Prokosch 1988) or in museum skins (Cramp & Simmons 1983, Marchant & Higgins 1993, Engelmoer & Roselaar 1998), apart from one study conducted on birds breeding on Sibiriakov Island, western Taimyr, where males were significantly longer in head-minus-bill, middle toe, head-plus-bill and tail lengths (Chylarecki & Sikora 1990). Hence, if bill and wing lengths are not sexually dimorphic, the presence of morphometrically different populations in different parts of Australia is confirmed.

Considering the theoretical and practical limits of POSCON predictions (cf. Tomkovich & Serra 1999), the following conclusions on the breeding origins of Australian Grey Plovers can be suggested: a) most of the NWA and SEA birds originated from the Eastern Siberian/Alaskan population, i.e. east of Lena River; b) birds coming from the discrete Wrangel Island population were more frequent in SEA; c) birds from western Siberia and Taimyr were virtually absent in Australia.

In NWA, the estimated body mass value for adults ready to migrate was similar to that calculated for South Africa (310 g, Serra *et al.* 1999); this suggests long non-stop flights on northward migration. With a fat load of 100 g, distances of up to 4200-5400 km could be covered without refuelling according to different flight range estimate formulae (Davidson 1984, Pennycuick 1989); birds could fly non-stop as far as northern Vietnam and the central Chinese coast. Although there was insufficient data to have a good estimate of an average SEA take off value, Grey Plovers probably accumulated more pre-migratory energy stores in SEA than in NWA. This difference has been observed in other medium/large waders (CDTM, pers. obs.) and suggests they may be making long non-stop flight direct to the Asian continent from SEA.

SEA birds apparently commenced body mass increase in February. Monthly body mass distributions in NWA (Fig. 2) suggested that in March adults were gaining mass but even the heaviest birds had not yet departed, while the negatively skewed distribution in April indicated that birds which had reached the threshold to commence migration had left the area.

Outside the period of pre-migratory body mass increase, adult Grey Plovers in NWA had body masses 6% lower than in SEA (Tab. 2). That birds wintering in the temperate regions of the northern hemisphere are heavier than those wintering in tropical areas was explained as an adaptive mechanism evolved to respond to unpredictable food resources, short day length and low temperatures (Blem 1990, Biebach 1998). Our data suggest that a similar latitudinal gradient is valid also for Grey Plovers wintering in temperate areas of the southern hemisphere, despite the fact that they experience the austral summer. The same pattern was observed on Great Knots *Calidris tenuirostris* and Red Knots *Calidris canutus rogersi* and linked to the more stable climate conditions of NWA (Barter 1987, Barter *et al.* 1988). In Africa, Grey Plovers wintering in a temperate area (Langebaan Lagoon, South Africa, 33°05'S, 18°02'E) were 9% heavier (Ruiters & Fokker 1998, Serra *et al.* 1999) and had higher basal metabolic rates (Kersten *et al.* 1998) than those wintering in the humid tropics (Archipelago dos Bijagos, Guinea Bissau, 11°40'N, 15°45W). This suggests that the effects of proximal factors on BMR and body mass, such as ambient temperature and photoperiod can be highly adjusted by birds to cope with local stress factors. A lower capacity of heat dissipation might explain why large-sized waders showed larger differences in body mass and BMR between humid tropical and austral temperate regions than small waders (see Kersten *et al.* 1998).

Primary moult durations in NWA and SEA were similar to those calculated for moulting areas located south of the northern tropic such as south-eastern India and South Africa (Balachandran *et al.* 2000, Serra *et al.* 1999) and *c.* 40 days longer than those observed in Europe (Boere 1976, Branson & Minton 1976, Serra & Rusticali 1998). It can therefore be supposed that Australia offers favourable conditions in terms of availability of trophic resources and time, so that moult can be spread over a long period (cf. Serra 1998). The starting dates of primary moult for NWA (10 September) and SEA (5 October) matches with arrival dates obtained by observations and count data, 10 September to end September in NWA and late September to first half October in SEA (CDTM, pers. obs.), thus confirming that Grey Plovers started primary moult soon after their arrival. The 25-days later start of SEA birds can be explained with the longer migration from the breeding grounds, an extra 2-3000 km.

No birds attained full breeding plumage before the onset of pre-breeding migration and over 80% of the birds left NWA in winter plumage or after having moulted less than 10% of the non-breeding feathers. This fact seems to be peculiar to Grey Plovers because all other Palearctic waders in NWA and SEA moult into almost complete breeding plumage before departure (CDTM, pers. obs.). In South Africa, 84% of Grey Plovers in

March and 55% in April had moulted less than one third of the non-breeding plumage (Serra *et al.* 1999). This difference would suggest that NWA Grey Plovers have a stricter time-scheduling for body moult before migration than South African birds, although there is no evidence of earlier departures from NWA. As for Grey Plovers following the East Atlantic Flyway, the rest of the breeding plumage seems to be attained later on in the season, when migrants have already reached stopover sites closer to the breeding quarters (Prokosch 1988, Ruiters & Fokker 1998, Serra *et al.* 1999).

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CHAPTER 8

PRIMARY MOULT, BODY MASS AND MIGRATION OF BRITISH GREY PLOVERS *PLUVIALIS SQUATAROLA*

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Ringing data on 6079 Grey Plovers Pluvialis squatarola *caught in Britain between 1959 and 1996 were analysed to describe their migratory strategies in relation with primary moult and body mass. Adults had a shorter and posticipated primary moult (duration 90 days, starting date 19 August) with respect to second-year birds (duration 109 days, starting date 5 June). Three categories of adults were identified on the basis of primary moult and body mass: (1) birds which did not moult, increased body mass and migrated further South, (2) birds which moulted 1-3 inner primaries, suspended, increased body mass and migrated, (3) birds which completed or suspended the moult and prepared to winter. In birds of the second category, timing of primary moult and body mass increase were overlapping. Among wintering birds, 38% was in suspended moult between P6 and P9. Ninety-six percent of birds in winter moult suspension were males and almost all completed the moult in spring. Grey Plovers left Britain in autumn with an average body mass of 280 g, enough to reach southern Morocco without refuelling. Both wintering adults and first-year birds showed a pre-winter body mass increase, peaking in December. Adults had a synchronised pre-migratory body mass increase in May, which suggested a negligible presence of African migrants. The average departure mass for spring migration, estimated at 316 g, allowed birds to fly non-stop to western Taimyr.*

INTRODUCTION

A close network of ecological, metabolic and energetic relationships between primary moult and body mass plays an important role in shaping the temporal and spatial organisation of migration. Where, when and how long-distance migrants moult and build up energy reserves are therefore essential information to understand migration patterns. It has been suggested that moult and pre-migratory body mass increase are temporally separated because of their energetic and metabolic costs (Payne 1972), but there is evidence that the two processes can overlap in many cases (Koopman 1986, Zwarts *et al.* 1990, Holmgren *et al.* 1993, Cherubini *et al.* 1996). An alternative hypothesis which considers the cost of carrying large deposits for a long time before departure as a possible explanation to mutual exclusion of the two events has been theoretically investigated (Klassen & Lindström 1996) and has found some empirical confirmation (Cherubini *et al.* 1996).

In this paper we analyse primary moult parameters and body mass variations of British Grey Plovers *Pluvialis squatarola*, trying to understand which adaptive solutions have locally and individually evolved and how they have interfered with migration and wintering strategies. A subset of these data was analysed 25 years ago and these earlier results have provided a useful background for methodological comparisons (Branson & Minton 1976).

The Grey Plover has a narrow latitudinal breeding distribution, restricted to the Arctic tundra of both the Old and the New Worlds, where it breeds in June-July (Byrkjedal & Thompson 1998). Outside the breeding season, it is a cosmopolitan species constrained to coastal wetlands, although large wintering populations are localised in temperate and tropical regions. Birds migrating along the East Atlantic Flyway probably originate from regions in Eurasia as far east as Taimyr and migrate as far south as the Gulf of Guinea. In Britain, it occurs throughout the year, but it is more abundant in August-September, and numbers are stable between October and May. In July, the population is formed by non-breeding birds (Branson & Minton 1976). During the last 30 years, numbers of wintering birds have steadily increased in Great Britain (Moser 1988, Tubbs 1991). Between 1981-1985 and 1988-1992, the wintering population increased from 21 250 to 43 200 individuals (Cayford & Waters 1996). As a rule, Grey Plovers have a complete moult in the wintering quarters; only a small proportion of males moult the innermost primaries during the last phases of the breeding period, starting from mid-July (Gromadzka & Serra 1998, Serra 1998). In the northern part of the wintering area, *c.* 30% of the birds suspend primary moult prior to the onset of hard weather (Branson & Minton 1976, Serra & Rusticali 1998, Serra 1998).

METHODS

This study is based on a sample of 6097 Grey Plovers caught for ringing in Britain from 1959 to 1996. This number includes 5539 first captures, 539 single or multiple retraps and 19 casualties. If not specified, analyses refer to first captures. Data from 242 birds found dead during cold spells in February-March 1991 were also available. These latter birds were sexed by dissection. The two data-sets were analysed separately.

Birds were aged according to plumage characters and moult status (Prater *et al.* 1979, Serra 1998). The following age categories could be recognised: first-years (birds in the first year of life, from arrival in October to 30 June of the following year), second-years (from 1 July of their second calendar year to the end of the first complete moult in September-November three to five months later), birds older than second year (from arrival in August to the end the primary moult in October-December) and adults (birds older than first-years, i.e. all birds after primary moult completion). After second-years complete their moult they are indistinguishable from adults.

Primary moult scores were recorded according to Snow (1966): old feathers were scored 0, new feathers 5 and growing ones from 1 to 4 in relation to their stage of growth. Primary feathers older than those of the previous moult, were scored 8. Raggedness score, i.e. the wing gap size corresponding to shed or growing feathers was calculated by the sum of 'missing' primary scores (e.g. 1, 2, 3, 4 for primaries scored 4, 3, 2, 1 respectively; Haukioja 1971). To investigate the role of primary moult in body mass regulation, we identified for each primary a limit in raggedness score which divided birds going to shed a primary from those going to suspend the moult. This threshold was set at the lower 95% confidence limit of the raggedness scores of birds going to shed a primary. These scores were calculated selecting birds with the outermost of the primaries in moult just shed or in pin (moult score = 1) and excluding the score of this outermost feather from calculations (Fig. 1).

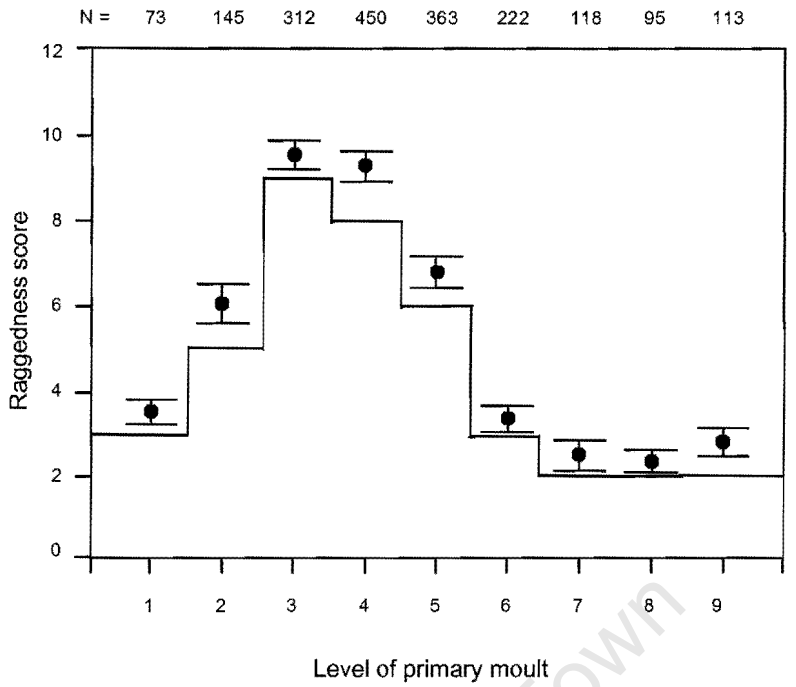

Fig. 1. Dots are average raggedness scores with 95% confidence limits of adults close to shed a primary at various moult levels. Raggedness score are calculated selecting birds with the outermost primary in moult just shed or in pin (moult score = 1) and excluding this feather from calculations. The broken line indicates the raggedness score integer closest to the lower 95% limit of each primary. This is assumed as the threshold to separate birds going to suspend the moult (values below the threshold) from birds which are going to shed a further primary (values above the threshold) at various levels of primary moult.

Moult scores 0(8) to 5 where converted to percentage feather-mass grown using the method described by Underhill & Joubert (1995), who also provided relative feather masses for Grey Plover primaries. Moult parameters were estimated using the model of Underhill & Zucchini (1988), data type 2. We assumed therefore that Grey Plover which moult in Britain, arrive with old primaries and stay for the winter. Birds in suspended primary moult and those which resumed it in spring were not used for the estimation of the parameters. Primaries were numbered from the innermost (P1) to the outermost (P10).

Body mass was recorded with spring balances to the nearest 1 g. Body mass frequency distributions with more than one mode were analysed by means of MIX 2.3, an interactive programme for fitting mixtures of distributions (Ichthus Data System 1988). We assumed that multi-modal distributions consisted of the sum of Normal distributions, i.e. that body mass distribution of each category of birds arriving in the study area, moulting or ready to migrate were Normal. We assumed also that the overall distribution of masses in an area where all birds which arrive store energy reserves and leave, is given by the sum of the distributions of the various cohorts of migrants and is therefore normal, provided that turnover and fattening rates are constant throughout the season.

RESULTS

Primary moult

On arrival in August-September, the suspension of primary moult by adults referred to two moult cycles: an early suspension of the cycle which had started at the end of the breeding season and a late suspension of the previous year moult. Out of 1077 birds older than second year, 54 (5%) were in suspended moult between P1 and P3 (Fig. 2), and five (0.5%) were in suspended moult between P7 and P9, indicating that, in these birds, the primary moult of the previous year was suspended before the onset of the winter and not completed in the following spring. Percentages did not change when considering a sample of 2521 adults caught in the same months, suggesting that almost no oversummering second-year birds were included in the adult category, because the inclusion of these birds, which do not suspend their first cycle of primary moult, would have changed these proportions.

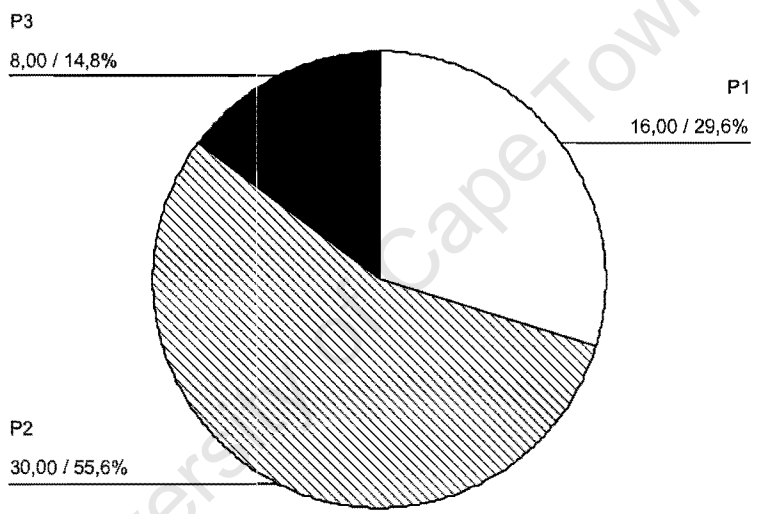

Fig. 2. Level of primary moult suspension of Grey Plovers caught during autumn migration in Britain.

Initiation of primary moult of second-year birds which summered in Britain was about 10 weeks earlier than that of adults arriving on migration (Table 1). Moult duration was 19 days longer in second-year birds than in adults, resulting in mean completion dates being separated by about seven weeks (Fig. 3a,b). The number of simultaneously growing primaries at various level of moult progress was larger in adults than in first-year birds, especially between P4 and P7 (Fig. 4).

In December-February, 38% of adults (N = 380) suspended primary moult between P6 and P9 (Fig. 5). The majority of birds resumed moult in March-April (Fig. 3b), but some birds had not completed primary moult before spring migration, and moulted the old outer primaries during the following post-breeding moult, as reported above. Indication of two moult *foci* simultaneously active or two concurrent moult cycles were found in five adults (Table 2). Primaries of the older generation (two years old) were shed when the moult of the newer primaries (one year old) reached P5-P7, i.e. 1-3 primaries before the limit of suspension of the previous year moult.

Among 162 birds which died during cold spells in February-March 1991, of which 85% were males and 15% females, 49 (30%) were in suspended moult. Forty-seven (96%) were males and two (4%) females.

Table 1. Primary moult parameters (dates or days) estimated for a sample of 720 second-year and 3320 adult Grey Plovers in Britain. Standard deviations are in brackets.

Parameter	Second-year birds	Adults
Mean starting date	5 June (3)	19 August (0.4)
Duration	109 (4)	90 (1)
Mean completion date	21 September (2)	17 November (1)
Standard Deviation	19 (1)	14 (0.2)

Table 2. Primary moult scores of adult and second-year Grey Plovers with two moult foci simultaneously active or indicative of two moult cycles.

	Date	Moult scores
Adults	22 August 1989	5555555031
	1 September 1991	5544200028
	17 September 1993	5555542048
	26 September 1988	5555443003
	27 September 1980	5555554202
Second-year birds	30 August 1980	2225555553
	30 August 1980	3455555543
	21 September 1986	4555555555

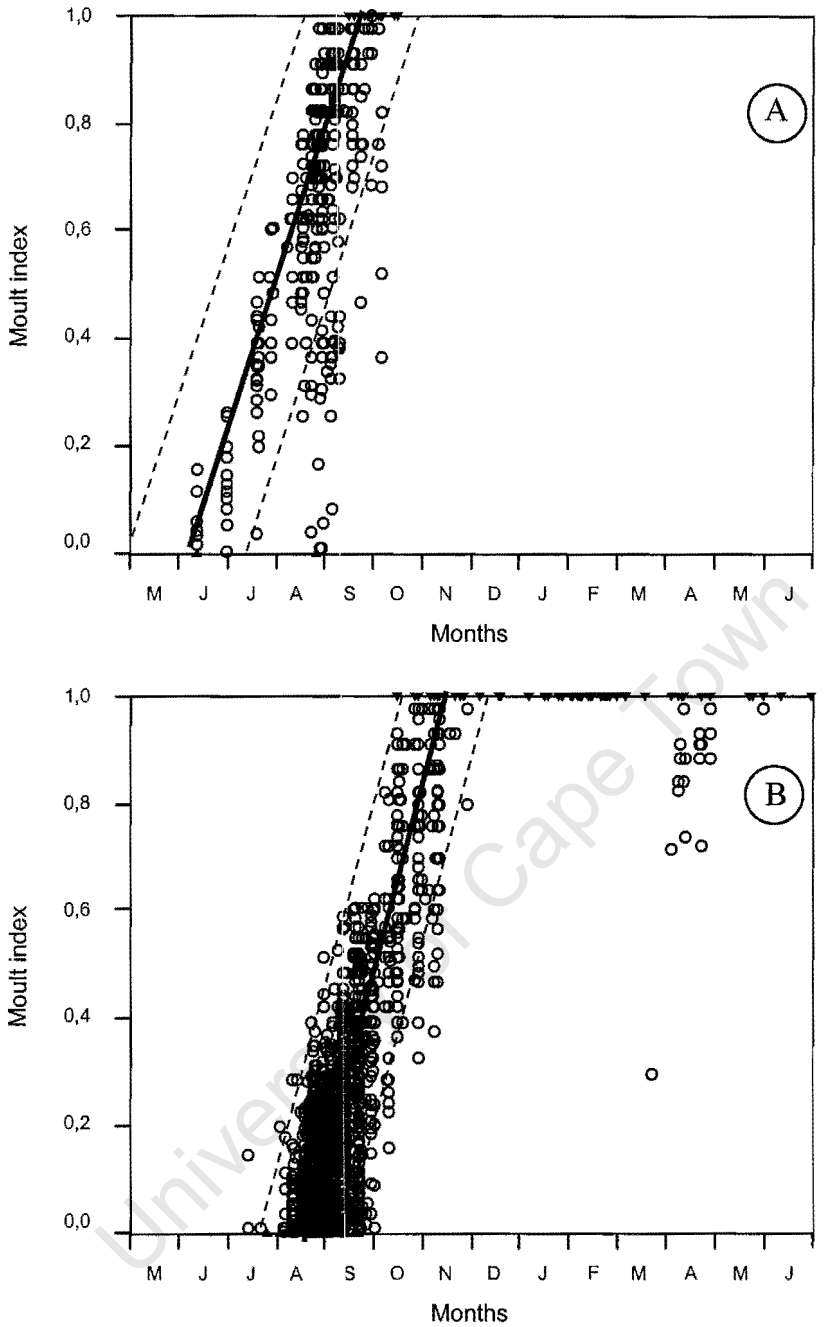

Fig. 3. Temporal distribution of primary moult index in first-year (A) and adult (B) Grey Plovers. The solid line is the average progression of the moult, the dashed lines include *c.* 95% of the population. Triangles are birds which have not started or finished the moult.

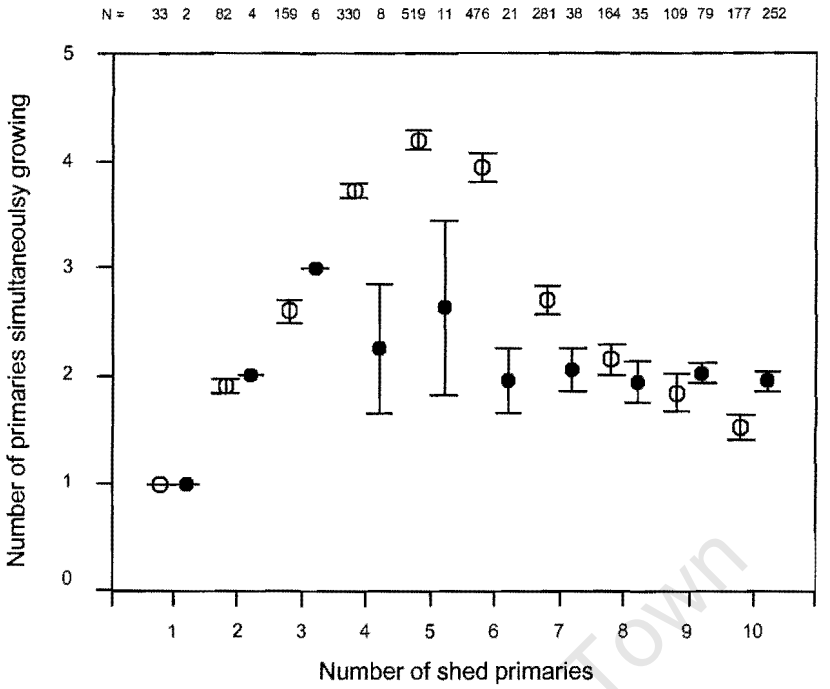

Fig. 4. Mean number of primaries simultaneously growing and 95% confidence limits in relation to the level of primary moult in first-year (circles) and adult (dots) Grey Plovers.

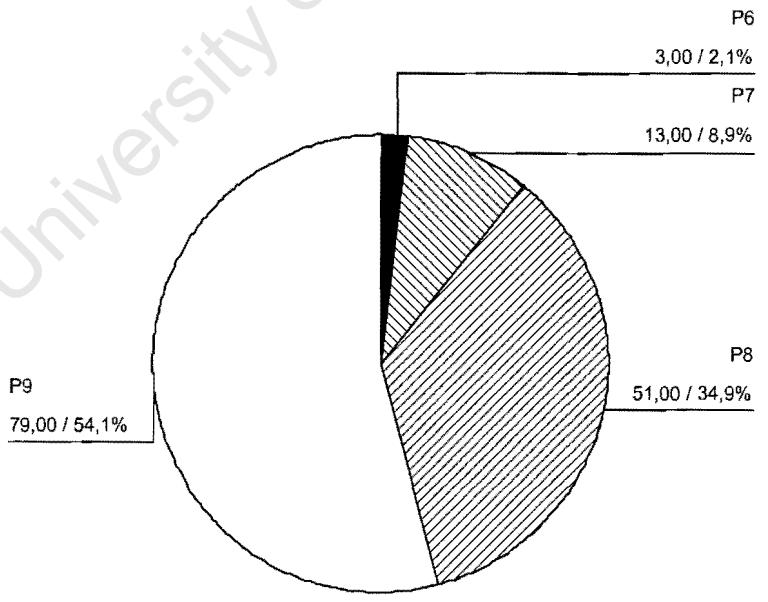

Fig. 5. Level of pre-winter primary moult suspension of adult Grey Plovers.

Body mass: seasonal variation and relationships with primary moult

On arrival in July-September, adults had an average mass of 222.9 g (SD = 18.9, range 166-330, n = 2459), similar to that of summering second-year birds (225.4 g, SD = 18.7, range 183-320, n = 452).

Body mass changed in relation to raggedness score and level of primary moult (Fig. 6). Between P1 and P3 birds going to suspend the moult had larger masses than birds going to shed a further primary. Between P4 and P7 there were no differences in body mass between the two bird categories, and the proportion of birds in a pre-suspension state was small (1-5%). From P8 onwards birds close to suspending moult had larger body masses than birds far from suspension or completion. Among birds far from suspension, body mass decreased from P1 to P3 by *c.* 4%, was stable between P3 and P9, and increased again by *c.* 4% from P9 to P10. Body mass differences among these 10 moult levels were significant ($F_{9,1956} = 10.9$, $P < 0.001$), but a homogeneous subsample given by the groups between P3 and P9 was identified (SNK test, $P < 0.05$). The average mass between P3 and P9 was 222.7 g (SD = 14.2, range 175-286, n = 1798).

Body mass frequency distributions of adults were bimodal when birds were grouped on the basis of three primary moult categories: (a) adults which had not started moult, (b) suspended at P1-P3, (c) in moult at P1-P3 (Fig. 7). The two components of each distribution were separated and their descriptive parameters calculated (Table 3). Comparing the means of the first components of the three categories, variations larger than 3% were found only between birds 'in moult at P1-P3' with the other two categories, and the same was for the second components.

For moult categories 'not started' and 'suspended at P1-P3', the observed bimodal distributions can be interpreted as the result of the subtraction of the normal distribution of masses of birds leaving the area to the hypothetical normal distribution of masses of all the birds which have stopped in the area. The first component is given by the birds which are not ready to migrate, the second one by the birds ready to migrate which have not yet departed and are accessible to sampling. An indication that the mean of the second component represents the mean departure value of each category is given by the fact that the mean of the means of the first and the second component falls close to the midpoint of the distribution ($\pm$ 10 g). The overall distribution might hence be generated by two components of equal proportions, featured by the same standard deviations and means equal to the estimated values. The average departure mass for autumn birds is estimated at 280 g.

For moult category 'in moult at P1-P3' the first component is supposed to be given by birds in moult, far from suspension and migration, and the second component by birds going to suspend and resume migration in a short time. This suggestion is supported by the fact that the observed proportions of these two categories at P1-P3 (70%, 30%), as defined in Figure 6, are similar to those estimated for the first and the second component (83%, 17%).

Outside moult and migration periods, the seasonal patterns of body mass of adult and first-year birds were featured by a December peak, averaging 270 g and 250 g respectively, followed by a steady decrease to reach *minima* in March (adult mean = 219.7 g SD = 20, range 184-300, n = 43; Fig. 8). Average mass of adults increased with respect to March of 4% in April (227.8, SD = 18.3, range 190-275, n = 45) and 44% in May (316.5 g, SD = 26.0, range 244-380, n = 37), while first-year mass did not vary. Because mass frequency distribution in May did not differ from normality (K-S test, $z = 0.7$, $p < 0.7$), and no mixed distributions were detected, we assumed 316 g as the average departure value.

Potential non-stop flights for autumn and spring migrations were 2970 and 4370 km (lean mass at take off 220 g, wing span 670 mm, aspect ratio 8; Pennycuick 1989).

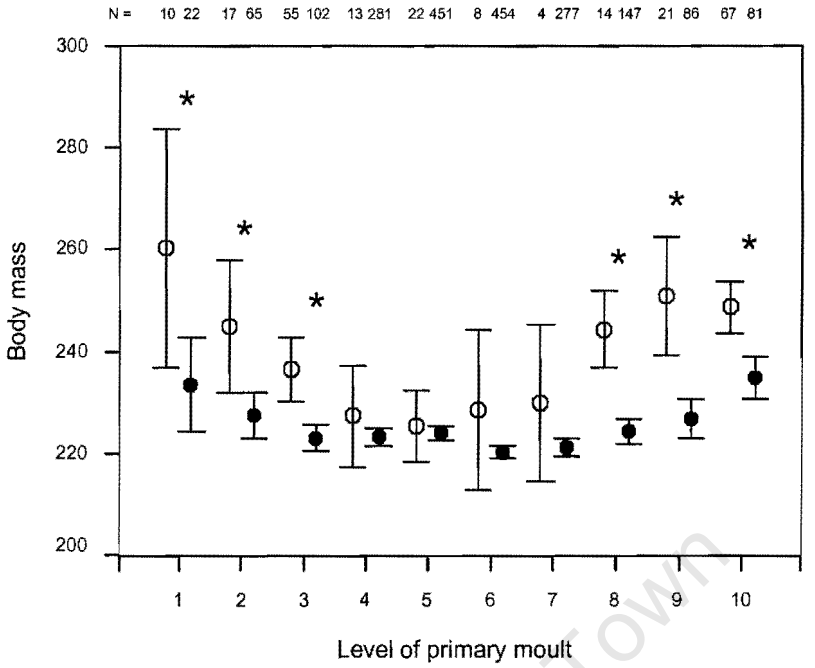

Fig. 6. Mean body mass (g) and 95% confidence limits in relation to the level of primary moult. Circles indicated birds going to suspend the moult, dots birds going to shed a primary with respect to limits showed in Fig. 1. * = differences significant at P < 0.01 between the two groups of birds at various moult levels (t-tests).

Table 3. Means, standard deviations and proportions (SD) of two-component frequency distributions of body mass (g) identified on three primary moult categories. Standard deviations are in brackets. The two components have been identified by means of the programme MIX (see Methods).

	1st component	2nd component	
moult not started	210.3 (1.17)	272.2 (6.5)	chi-sq. = 12.4
n = 367	15.4 (0.9)	284.7 (4.3)	d.f. = 11
	0.83 (0.03)	0.17 (0.03)	P = 0.3
moult suspended between p1-p3	216.3 (2.1)	284.7 (8.5)	chi-sq. = 7.5
	18.4 (1.6)	18.1 (6.3)	d.f. = 10
n = 128	0.89 (0.04)	0.11 (0.03)	P = 0.7
in moult between p1-p3	224.3 (1.9)	265.5 (16.2)	chi-sq. = 5.89
n = 271	13.9 (1.3)	(7.6)	d.f. = 7
	0.83 (0.1)	0.17 (0.1)	P = 0.6

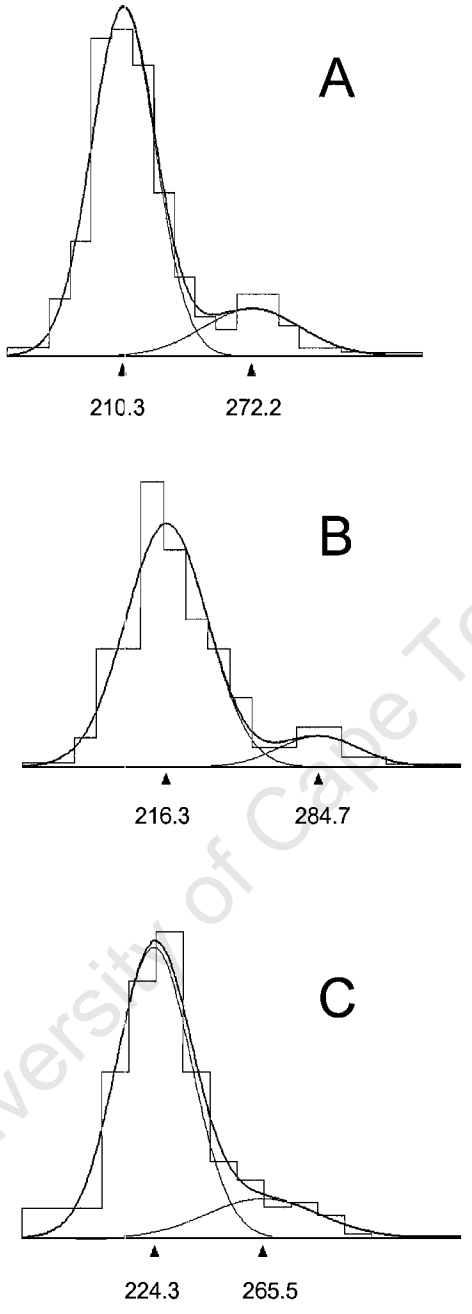

Fig. 7. Frequency distributions of body mass (g) of Grey Plovers at three moult stages. Birds which have not started the moult (A), in suspended moult between P1-P3 (B), and in moult between P1-P3. Two normal curves and their resultant were fitted for each distribution. Triangles indicate the means of the normal curves. The parameters of the normal distributions are in Table 3.

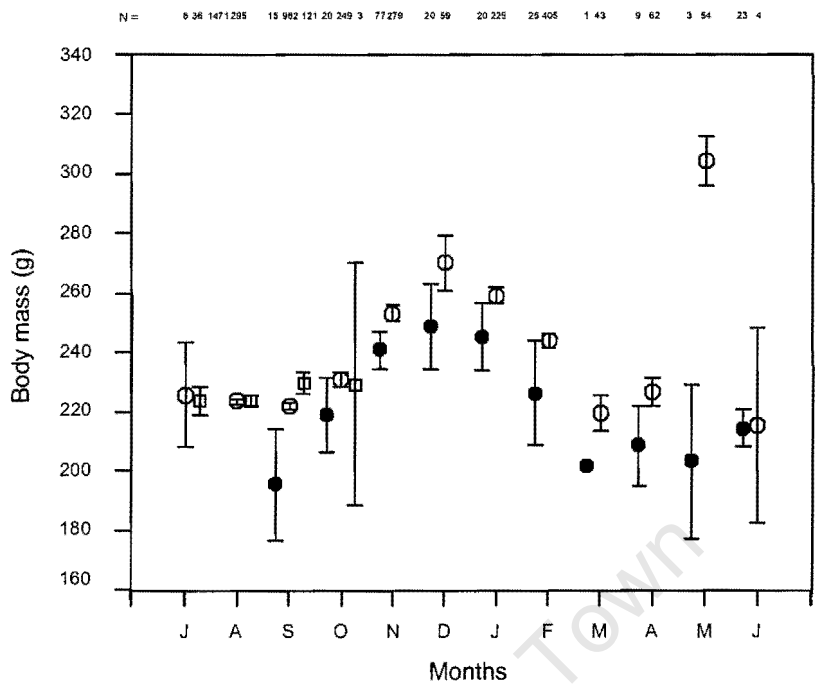

Fig. 8. Monthly distribution from July to June of body masses of adults (circles), first-year (dots) and second-year birds (squares). Means and 95% confidence limits are shown.

DISCUSSION

Primary moult

The proportion of adults (5%) found in Britain with 1-3 new inner primaries was smaller than that observed at a stop-over site on the Baltic coast during post-breeding migration (11%, Gromadzka & Serra 1998), possibly because of a rapid resumption of moult, as suggested for other moulting and wintering sites (Serra & Rusticali 1998, Serra *et al.* 1999). However, a direct comparison of these two values cannot be made, because the British group includes both birds which have started the moult on the breeding grounds and those which have started and suspended in Britain (see below). Using a subset of the data presented here (i.e. for the period 1959-1974) and considering also birds in moult but with indications of a recent moult resumption, Branson & Minton (1978) estimated that the proportion of birds arriving in suspended moult in August was 25-40%. However, the latter method possibly over-estimates the percentage of suspension due to the difficulty of inferring recent suspension from active moult. Data from breeding grounds are too scanty for reliable comparisons, especially if sex-differences and early/late breeders are considered (see Gromadzka & Serra 1998), so that proportions from stop-over sites probably give the best estimates.

Primary moult parameters of adults calculated with the model of Underhill & Zucchini gave results almost identical to those obtained by fitting the median dates of the population for different moult scores: duration 90 days, starting date around mid-August (Branson & Minton 1978). Primary moult duration was three days shorter than that found in north-eastern Italy (Serra & Rusticali 1998) and 30-40 days shorter than at sites having mild winters (Serra *et al.* 1999, Balachandran *et al.* 2000, Minton & Serra 2001, Pearson & Serra 2002).

The first cycle of primary moult in second-year birds was temporally segregated from that of adults and 19 days longer. However, it was 84 days shorter (43%) than in South Africa, where moult started on 19 April and finished on 20 October, and spread throughout the whole period of adult absence (Serra *et al.* 1999). The shorter duration of moult in Britain can be interpreted as a response to a shortening daylength from 21 June onwards in the northern hemisphere, i.e. for 3/4 of the moult period. A reduction in day length has been demonstrated to accelerate moult rate in several species (Noskov & Rymkevich 1985, Dawson 1994, 1998, Noskov *et al.* 1999).

The great majority of adults which had pre-winter moult suspension completed the moult in spring, before migration, suggesting a high selective pressure to migrate with new primaries. Pre-winter moult suspension seems to be typical of males. A simple explanation is that males usually attend the brood on the breeding grounds and hence start migration and primary moult 2-3 weeks later than females (Byrkjedal & Thompson 1998). The larger proportion of males wintering in Britain, despite their delayed migration and moult, suggests the existence of high selective advantages in wintering at northern latitudes for males. An earlier arrival on the breeding grounds or better physical conditions (Sandberg 1996) might explain this pattern.

Some second-year birds had two primary moult cycles concurrently active and the proportion of these birds was certainly underestimated due to plumage resemblance to older birds. The two cycles indicate that early in the season primary moult is not inhibited by any endogenous or exogenous cue which appears only at the time adults complete their moult cycle and might be identified in daylength (Noskov *et al.* 1999). Timing of primary moult of second-year birds seems therefore to be regulated on adult circannual rhythms, suggesting that both the early start and the second cycle might be maladaptive (Serra *et al.* 1999).

Body mass

As a rule during autumn migration, Grey Plovers arrive in Britain and north-western Europe with all primaries old or with the moult suspended at P1-P3. Among these birds we identified three groups: (a) birds which increase body mass without starting or resuming primary moult and rapidly move further south; (b) birds which moult 1-3 inner primaries in Britain, suspend and migrate; or (c) birds which complete the moult and prepare to winter in Britain or neighbouring coasts. Mass frequency distributions suggest that birds start or resume primary moult in a short time after their arrival, because we were not able to detect the component of birds which were going to moult in Britain within the group of birds which had not yet started moult. Hence, body mass increase follows or is concurrent to the onset of the moult.

Body mass increase, either pre-migratory or pre-winter, seems to be compatible with primary moult (Fig. 6). Some birds going to suspend the moult before migration started pre-migratory fattening when they had still large gaps in the wing, probably pressed by the need of minimising the duration of fattening (Klaassen & Lindström 1996) or migration (Alerstam & Lindström 1990, Lindström & Alerstam 1992, Weber *et al.* 1994, 1998). Birds going to winter kept the two processes separated till the last stages of moult, putting on reserves when they were going to suspend or finish the moult. Only those renewing the last primary had a slight mass increase when still far from moult completion. Similar patterns of partial overlap between primary moult and pre-migratory mass build-up were previously described in other Charadriiformes (Ruff *Philomachus pugnax*: Koopman 1986, Little Tern *Sterna albifrons*: Cherubini *et al.* 1996, Black Tern *Chlidonias niger*: Zenatello *et al.* submitted). Grey Plovers are therefore able to simultaneously fulfil both metabolic and energetic costs of body mass increase and primary moult if it is required by migration time schedules.

The estimated flight range of *c.* 3000 km estimated for autumn migration would allow Grey Plovers which have replenished energy reserves in Britain to fly bordering the Atlantic coast of Europe and Africa as far as southern Morocco in a single jump. Unfortunately, there are no ringing recoveries to support this or other hypotheses.

The seasonal patterns of body mass variation in first-year and adult birds did not differ from those obtained in previous studies on British Grey Plovers (Branson & Minton 1976, Johnson 1985). They have a clear peak of energy reserves in December, typical of birds which try to get an insurance against a period of severe weather (Biebach 1996, Pienkowski *et al.* 1984) (Fig. 8). The increase in percentage body mass with respect to the lowest monthly averages (20%) is higher in Grey Plovers than in any other wader wintering at the Wash, possibly because low temperatures strongly affect prey availability for visual foragers (Johnson 1985). In Italy, there was a similar seasonal pattern for both adult and first-year birds (Serra & Rusticali 1998). However, in Italy adults were 7% leaner at mid-winter peak, possibly because of milder winters or more predictable feeding conditions (Serra & Rusticali 1998).

Short movements at the end of the moult have been ascertained by some ringing recoveries but they should not influence body mass patterns. Branson & Minton (1976) mentioned the recovery in France of one bird which had finished primary moult eleven days before at the Wash. However, there are no recoveries to indicate that some birds migrate to African winter quarters at the end of the moult. The same is probably true also for Grey Plovers moulting at the Wadden Sea (M. Engelmoer pers. comm.).

There is a synchronised timing of mass increase in May, suggesting a negligible influx of birds arriving from southern winter quarters. Movements along the East Atlantic Flyway in spring seem to strictly follow the western coast of continental Europe along a narrow path, excluding inland routes crossing central Europe to the East, and Britain and Ireland to the West (Byrkjedal & Thompson 1998, Exo & Wahls 1996). British birds which move to the Wadden Sea in spring (Meltofte *et al.* 1994), probably leave the wintering area in March or April, before having started to build up energy reserves. The departure of birds at different stages of mass build-up in May would have resulted in a multi-modal frequency distribution of masses. The estimated flight range for spring migration (4370 km) would enable Grey Plovers to reach breeding areas located as far away as western Taimyr with a single non-stop flight.

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CHAPTER 9

DURATION OF PRIMARY MOULT AFFECTS PRIMARY QUALITY IN GREY PLOVERS *PLUVIALIS SQUATAROLA*

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Feather wear is the natural degradation and breakage of feather structure during the interval between moults. Different rates of feather wear have been observed for primaries of free-living populations of several species of passerines and waders, and this variability has been linked to different concentrations of melanins. In this study primary moult duration explained 59% of the variation in annual rates of primary abrasion (percentage wing length loss) of seven Grey Plover wintering populations, while migration distance explained 14%. The analysis suggests that primary moult duration plays a key role in determining primary durability and hence primary quality. Long distance migrants might evolve more durable primaries, despite the higher predation risks and energetic costs of a prolonged moult. Partial or complete pre-breeding primary moults of first-year waders and complete biannual moults of some passerines might have evolved under selective forces favouring migration with unabraded primaries.

INTRODUCTION

The chemical and physical processes that underlie feather wear, which is the result of fractured and lost barbs and barbules and loss of the distal rachis, are poorly understood, although physical (Bergman 1982) and bacterial (Burtt & Ichida 1999) degradation play a role. Mechanical stress might also be involved, although experimental evidence is still lacking (Bonser 1996). The durability of keratin, the structural protein of feathers, is directly related to the presence of melanin (Averill 1923, Barrowclough & Sibley 1980, Bergman 1982, Burtt 1986, Burtt *et al.* 1998). Melanic keratins may be harder than non-melanic keratins because: (i) melanic keratins are thicker than non-melanic keratins, and can therefore sustain more abrasion, (ii) melanin is incorporated in feathers as granules surrounded by keratins, and granular fillers enhance abrasion resistance (Voitkevich 1966, Bonser 1995, 1996).

Several studies have provided empirical evidence of primary feather wear in free-living populations by calculating the decrease of wing length (e.g. Nisbet 1967, Norman 1980, Leverton 1989). In waders (Charadrii), the following reductions of average wing lengths between birds with old and new primaries have been reported: Grey Plover *Pluvialis squatarola*, 0.5% in Britain (Branson & Minton 1976), Sanderling *Calidris alba*, 1% in South Africa and 2.5% in Britain (Summers *et al.* 1987), Redshank *Tringa totanus*, 2% in Britain (Summers *et al.* 1988), Turnstone *Arenaria interpres*, 1.6% in Scotland and 3.2% in South Africa (Summers *et al.* 1989), Ruff *Philomachus pugnax*, 2.5% in Kenya, Knot *Calidris canutus*, 4% in Britain (Pienkowski & Minton 1973). The differences observed among species and populations are unexplained.

Variables affecting feather abrasion can be divided into: (i) external factors, which include mechanical abrasion linked to flight, rubbing against vegetation or other objects, degradation of keratins by exposure to

photochemical processes (Bergman 1982) or degrading ectoparasites, bacteria and fungi (Burtt & Ichida 1999), and (ii) physiological factors associated with abnormal feather formation and nutrition (Murphy 1996). In this paper, I assume that a slower moult allows the deposition of more melanin, because the amount of pigment in a feather is inversely proportional to its growth rate (Voitkevich 1966). More melanin might enhance primary durability and hence primary quality, at least for long-distance migrants, because the maintenance of the original length and shape of primaries is critical to their flight performance (Barrowclough & Sibley 1980) and hence to survival. The importance of feather quality in determining the timing of moult was recently suggested by Holmgren & Hedenström (1995). Resistance of the primaries to wear can therefore be assumed to be an index of primary quality. This paper aims at evaluating the importance of primary moult duration and length of migration journey on the annual rate of primary abrasion in the Grey Plover. In this species, a circumpolar breeding wader with a cosmopolitan winter distribution, primaries and most of the body feathers are renewed at the end of the post-breeding migration, and a partial pre-breeding moult starts in most populations shortly before spring migration (Byrkjedal & Thompson 1998).

METHODS

Primary resistance to wear is expressed here as the relative reduction in wing length during the period of almost one year from immediately after one primary moult to immediately before the next. This is referred to as percentage wing length loss (PWLL).

Wing length and primary moult data were obtained from adult Grey Plovers caught for ringing in seven wintering areas: Britain, Italy, India, Kenya, South Africa, NW Australia and SE Australia (Table 1). The difference between the PWLL value calculated by Branson and Minton (1976) and that used here is due to the fact that I have selected wintering birds (December-February). Moult durations were calculated with the model of Underhill & Zucchini (1988) and Underhill *et al.* (1990). For calculations, primary moult score was converted in a moult index based on percentage feather-mass grown estimated from the relative masses of primaries (Underhill & Joubert 1995). Wing length was measured according to Evans (1986). An estimate of the migration journey for each population was given by the loxodromic distance between the wintering site and the breeding range.

Table 1. Wing lengths (mm), primary moult durations (days) and migration distances (km) of seven Grey Plover wintering populations. Migration distances are loxodromic distances between wintering site and the closest area of the breeding range.

	'New' wing length, SD	'Old' wing length, SD	Wing length loss	Duration of moult	Migration journey	Source
Great Britain (GB)	202.9 (4.2) n = 143	200.8 (4.3) n = 56	2.1 (1.0%)	90	4000	BTO unpubl. data
Italy (It)	206.2 (3.3) n = 17	202.9 (4.3) n = 24	3.3 (1.6%)	93	5000	Serra & Rusticali 1998
India (In)	204.1 (5.9) n = 189	202.8 (5.2) n = 50	1.3 (0.5%)	127	8000	Balachandran *et al.* 2000
Kenya (Ke)	201.8 (4.6) n = 17	201.1 (4.7) n = 28	0.7 (0.4%)	130	10000	Pearson & Serra 2002
South Africa (SAf)	204.9 (6.7) n = 124	203.5 (6.2) n = 72	1.4 (0.7%)	131	14000	Serra *et al.* 1999
NW Australia (NWA)	206.0 (4.6) n = 99	204.8 (5.2) n = 47	1.2 (0.6%)	121	10000	Minton & Serra 2001
SE Australia (SEA)	208.9 (3.7) n = 15	207.8 (4.9) n = 76	1.1 (0.5)	128	13000	Minton & Serra 2001

RESULTS AND DISCUSSION

The duration of primary moult of Grey Plovers ranges between 90 and 131 days (Table 1). The short moult durations (90-93 days) observed in Britain and Italy are probably determined by time constraints linked to the need to complete the moult before the arrival of severe weather conditions, while the long moult durations observed farther south in the non-breeding range are probably constrained only by departure dates, because the onset of the pre-breeding moult and pre-migratory body mass gain are linked to the completion or suspension of the primary moult (Serra *et al.* 1999).

Because migration distance and moult duration were highly correlated, partial correlation coefficients were calculated to explain the effect of these two variables on PWLL (Table 2). Migration distance had less impact on feather abrasion than moult duration, explaining respectively, 14% and 59% of PWLL variance (Fig. 1). Both partial correlations were non-significant, possibly because of the small sample size, seven values. With unchanged partial correlation coefficients, the 5% significance level would be reached with a sample size of eight for moult duration (two-tailed test) and 21 for migration distance (one-tailed test).

Table 2. Correlation coefficients between percentage wing length loss (PWLL) and migration distance and moult duration are given above the diagonal, partial correlation coefficients below the diagonal. * = one-tailed test; ** two-tailed test.

	PWLL	Migration distance	Moult duration
PWLL	-	-0.65	-0.85
		P = 0.06*	P = 0.02**
Migration distance	0.38	-	0.88
	P = 0.2*		P = 0.01**
Moult duration	-0.77	0.81	-
	p = 0.07**	P = 0.05**	

The higher resistance of primaries moulted at slow speed suggests that a longer moult duration produces feathers of better quality and that feather quality might have played a key role in shaping moult strategies in relation to ecological factors (Holmgren & Hedenström 1995). Migration requirements might be linked to pre-breeding moult of outer primaries in first-year waders, and it has been suggested that selection favours migration with new primaries in long distance migrants (Prater 1981, Serra *et al.* 1999). In some populations of Willow Warbler *Phylloscopus trochilus*, post-breeding moult is half as long as pre-breeding moult (Underhill *et al.* 1992, Svensson & Hedenström 1999). Short post-breeding moults might produce feathers of low quality whose keratin structure degenerates before the pre-breeding migration and this might have given rise to the evolution of a second moult cycle. Differential insulation needs and physiological constraints have been suggested to explain the long pre-winter and the short pre-summer moults in the Black-chested Prinia *Prinia flavicans* (Herremans 1999). Partial or complete pre-breeding moult in first-year birds, and complete biannual moults might therefore have evolved under different selective forces linked to migration distance, pigment deposition, feather structure and moult duration.

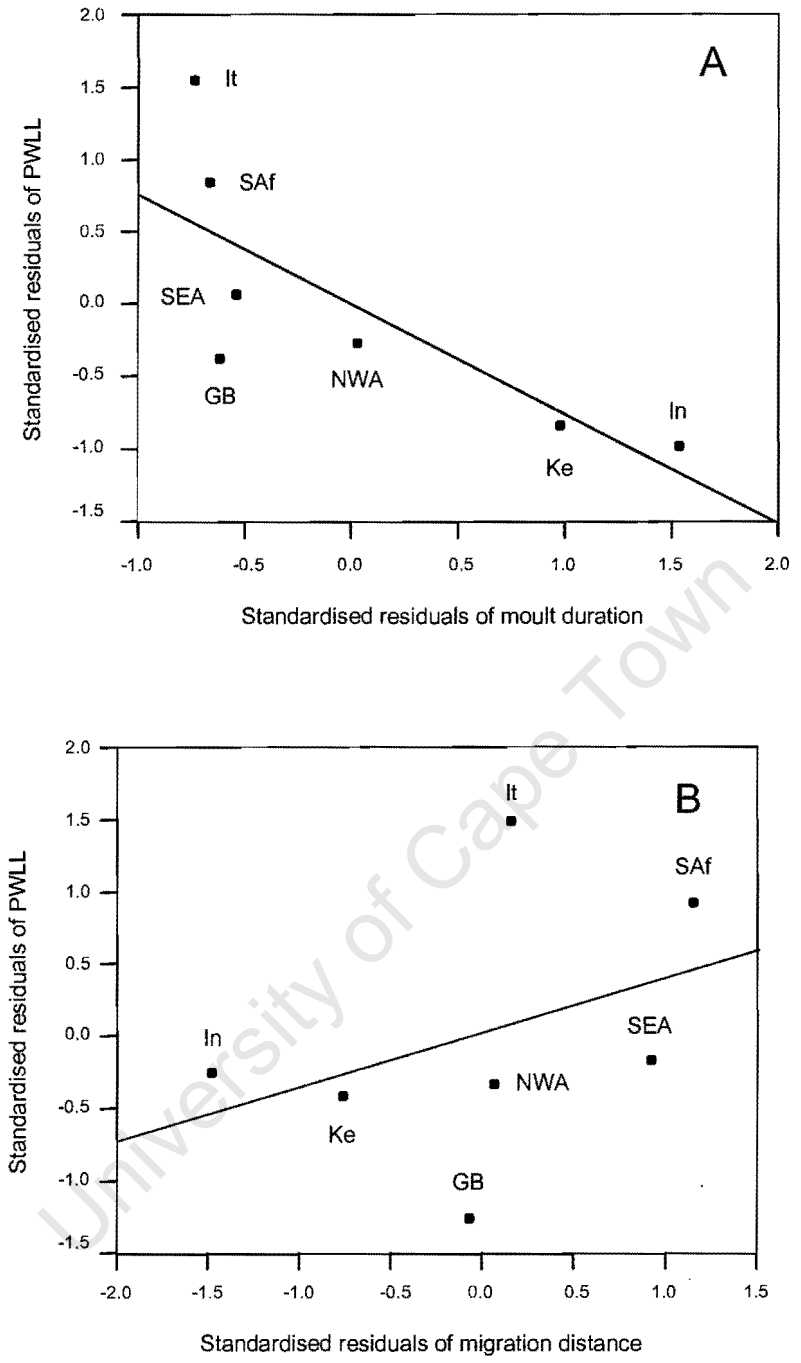

Fig. 1. Percentage wing length loss (PWLL) of Grey Plovers *Pluvialis squatarola* during the inter-moult period (A) in relation to duration of moult corrected for the effect of migration distance and (B) migration distance corrected for the effect of duration of moult. A regression line is fitted to the points. Codes for localities are given in Table 1.

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CHAPTER 10

CONTRASTING PRIMARY GROWTH RATES AND PRIMARY MOULT DURATIONS IN FAST AND SLOW MOULTING POPULATIONS OF GREY PLOVERS: INDIVIDUAL PLASTICITY OR EVOLUTION OF MOULT STRATEGIES?

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Primary moult data from adult Grey Plovers Pluvialis squatarola *caught for ringing at seven wintering areas were analysed. The method of Underhill & Zucchini (1988) was applied to the moult index of the ten primaries as a whole as well as to those of primaries taken individually. Five populations had a slow primary moult (Kenya, South Africa, India, NW Australia and SE Australia), and two a fast moult (Britain, Italy). Different moult durations were obtained by the simultaneous shedding of a variable number of primaries and by regulating feather growth rates. The duration of the moult of each primary (P1-P10) was calculated for an assemblage of birds given by the slow moulting populations and for the British fast moulting birds. The duration of moult of each primary did not significantly differ between P1 and P10 in slow moulting birds and between P1 and P8 in fast moulting birds. Among the latter group, moult durations of P9 and P10 were significantly shorter than those of the innermost primaries. Mass and length of primaries were linearly correlated to calamus diameter. The percentage variation explained increased by 4% and 15%, respectively, by excluding the longest primary. The relationship between primary growth rate (daily percentage feather-mass grown) and total primary length is linear between P1 and P9 in slow moulting birds, and quadratic between P1 and P8 in fast moulting birds. The average total daily percentage feather-mass grown increased linearly from P1 to P5 both in fast and in slow moulting populations. Feather mass production was not constant throughout the whole moult period but it was regulated by proximate needs. However, in slow moulting birds, mass production was constant between P6 and P10, i.e. when 72% of total primary feather mass had been produced. This explains why feather-mass transformations are effective in increasing linearity of moult score distributions. The period free from energetically costly events was longer at inter-tropical latitudes, and decreased moving both north- and southwards. It is suggested that primary moult duration and feather quality contribute to explain why the barycentre of winter distribution is the inter-tropical zone. Primary moult patterns observed in Europe should be considered as individual adaptations to a new environment because they seem regulated by external factors.*

Introduction

Primary moult is a major event in the annual cycle of birds and it crucially affects their life histories. However, the state of the art is far from that of other main avian issues such as breeding and migration. Most relevant moult studies have focused on the energetic and nutritional aspects of feather replacement (Murphy & King 1991, Dietz *et al.* 1992, Lindström *et al.* 1993) and on the aerodynamics of an incomplete wing area (Chai 1997, Chai *et al.* 1999, Swaddle & Witter 1997, Tucker 1991). A limitation to the improvement in knowledge of moult

variation, identification of adaptive patterns and development of a phylogenetic approach has been the lack of an efficient descriptive method, despite the pioneer work of Streseman & Streseman (1966) and Newton (1966, 1967, 1968, 1969) and the vast array of studies concerning timing, rate and patterns of moult that have regularly appeared since the late 1960s (e.g. Evans 1966, Morton *et al.* 1969, Haukjoia 1971; for reviews see Prater 1981, Ginn & Melville 1983, Jenni & Winkler 1994). This weakness originated from the analysis of field data, conventionally recorded on wild birds by scoring each feather from 0 (old) to 5 (new) and giving intermediate scores in relation to growth stage (Snow 1967). The sum of these scores for the primaries of one wing, the so-called 'moult score' has a non-linear increase rate with time. Furthermore, moult scores are truncated at 0 until moult actually commences, and at 50 once moult is completed. This precludes a rigorous application of standard linear regression methods (Pimm 1976, Summers *et al.* 1983). Such regressions give the duration of the moult period in the population as a whole rather than the average duration of moult in single individuals and also ignore the non-moulting component of the population (Underhill & Zucchini 1988). A result closer to the average individual moult duration could be obtained by assuming time to be the dependent variable on moult score but sampling dates are usually non-randomly selected and the method should hence be rejected (Underhill & Zucchini 1988). This methodological impasse was solved by a maximum-likelihood model which had only three assumptions: i) constant increase of moult score rate with time, ii) same moult duration for each bird, iii) daily moult score samples are representative of the population (Underhill & Zucchini 1988, Underhill *et al.* 1990). In this model, moult scores were transformed in an index of percentage feather-mass grown (moult index) to improve linearity with time (Summers *et al.* 1983, Underhill & Zucchini 1988). An analysis based on moult scores of individuals captured twice during the same moult revealed that only data categorising bird as 'moult not started', 'in moult' or 'moult completed' (data-type 1, Underhill & Zucchini 1988) gave unbiased estimates of moult parameters, while the additional information of individual moult scores (data-type 2), or the exclusive use of moult scores of birds in moult (data-type 3) determined under-estimations of the moult duration (Newton & Rothery 2000). However, these results can be partially explained because Newton & Rothery (2000) did not transform moult scores into percentage feather-mass moult indices to improve linearity (Underhill in press).

The Grey Plover *Pluvialis squatarola* is an Arctic wader with a cosmopolitan winter distribution (Byrkjedal & Thompson 1998). Following the ecological definition of Alerstam & Hogsted (1982), the Grey Plover is a typical S-species, because its life history shows adaptations to ecological restrictions and possibly to high intra-specific competition on the breeding grounds: it has a small clutch size, a deferred age of first breeding, an early migration outside the breeding grounds, a post-breeding and post-migration moult ('winter moult'), and a differential migration with adults moving ahead of juveniles (Cramp & Simmons 1983, Paulson 1995, Byrkjedal & Thompson 1998, Gromadzka & Serra 1998, Serra 1998).

Populations wintering on four different continents offered the opportunity to test the effect of migration distance and environmental conditions on the appearance and evolution of primary moult patterns. The aim of this paper is to characterise primary moult in Grey Plovers originating from various wintering areas, which are known to have different moulting durations: slow moulting populations in areas with mild winters and fast moulting populations in areas with cold winters (Serra 1998). The model of Underhill & Zucchini (1988) was applied to the moult index of birds belonging to seven populations and to that of each of the ten primaries taken one by one in order to calculate the duration of the moult for each primary. The relationships of primary length and mass with primary growth rates were also explored.

Methods

Ringing data from seven moulting and wintering sites (Britain, Italy, Kenya, South Africa, India, NW Australia and SE Australia) were analysed. Moult parameters for these populations (Serra 2001) were calculated using the model of Underhill & Zucchini (1988), and subsequent developments (Underhill *et al.* 1990, Underhill *in litt.*). This model assumes five possible scenarios given by: i) bird presence in the study area and their following availability to sampling, and ii) type of moult data collected (moult scores recorded for each bird or only moult conditions available, i.e. moult not started, in moult, moult completed). An unpublished version of the model allows to consider at the same time both birds with full details of moult scores and those for which only the information on moult conditions is available. Data-types selected for each population are in Table 1.

Since moult durations in Kenya, South Africa, India, NW Australia and SE Australia populations did not differ (Table 1), these birds were merged into a single group in order to have a sample of slow moulting individuals to be compared with the large British sample of fast moulting birds. Dates of capture of individuals originating from the various populations were translated to a common origin (day 0) using the mean starting dates of their respective populations.

The Underhill & Zucchini model (1988) was also applied to calculate moult parameters of the primaries of slow and fast moulting populations taken one by one. The first assumption of the model in this case was that growth rate is constant for each primary. A trend close to linearity in the growth rate of individual primaries is already known for passerines (Newton 1967) and for waders (Sach 1968). Transformations of primary scores of individual feathers into percentage feather-mass grown or percentage feather-length grown was unnecessary, they were simply standardised from 0 to 1 by dividing the moult score of the feather by 5.

The 10 long primaries were numbered from the innermost (P1) to the outermost (P10). Primary length was measured with a dial calliper (accuracy 0.1 mm) on flattened and stretched feathers. These were extracted from one adult Grey Plover with recently renewed primaries. The bird had been shot by poachers in Italy on 20 October 1998 and was deep-frozen till March 2001. The total primary length, i.e. the chord from tip of the rachis to base of the calamus, was measured. Percentage primary masses were taken from literature (Underhill & Joubert 1995). The daily percentage feather mass production is the relative feather mass produced by each primary during each day of moult assuming a constant growth rate. The size of feather follicles was estimated as the maximum diameter of the calami measured with a dial calliper (accuracy: 0.1 mm) within 10 mm from the tip of the base.

Because the Grey Plover breeds on a narrow latitudinal band of the Arctic tundra, it has been assumed that adults from various Palearctic populations arrive and leave the breeding grounds approximately on the same dates (see Fig. 7.1 in Byrkjedal & Thompson 1998). Arrival date was set on 1 June, departure date on 15 July. Numbers of wintering populations in the Afro-Palearctic migratory system were estimated from references and other sources listed in Appendix 1.

Results

Moult parameters of the five slow moulting populations (Kenya, South Africa, India, NW Australia and SE Australia) did not differ from those of the population obtained by their clustering. Slow and fast (Britain and Italy) moulting populations differed at the 0.05% significance level (Table 1).

Table 1. Primary moult parameters of seven Grey Plover populations. Parameters of slow moulting populations were estimated from a sample of all individuals of groups 2-7. Data-type refers to categories used for the model of Underhill & Zucchini (see methods).

Wintering site	Data-type	Duration (SD) 95% CL	Starting date (SD) 95% CL	Completion date (SD) 95% CL	Standard Deviation (SD) 95% CL
Great Britain (GB)	2	90 (1) 88-92	19/8 (0.4)	17/11	
Italy (It)	2	93 (8) 77-109	18/8 (6)	19/11 (4)	22 (3)
India (In)	2	127 (8) 111-143	1/9 (7)	5/1 (3)	29 (2)
Kenya (Ke)	1/2	130 (4) 122-138	13/9 (2)	19/1 (3)	25 (2)
South Africa (SAf)	2	131 (6) 119-143	30/9 (6)	8/2 (4)	28 (2)
NW Australia (NWA)	5	121 (5) 118-131	10/9 (2)	9/1 (4)	12 (1)
SE Australia (SEA)	2	128 (6) 116-140	5/10 (3)	9/2 (5)	16 (1)
Slow moulting populations	2	136 (3) 130-142	26 (2)		26 (1)

Grey Plovers moulting at a fast rate had a larger number of primaries simultaneously growing than those moulting at a slow rate, especially in the feather tract P4-P7 (Fig. 1). The duration of moult of each primary did not significantly differ between P1 and P10 in slow moulting birds and between P1 and P8 in fast moulting birds. Moult durations of P9 and P10 were significantly shorter than those of the innermost primaries in fast moulting birds and those of the P9 and P10 in slow moulting birds (Table 2).

Table 2. Duration of moult of primaries in slow and fast moulting populations. ** = difference significant at the 5% level.

	Duration (SD) 95% Confidence limits		
	Slow	Fast	P
P1	31 (4) 23-39	28 (1) 26-30	NS
P2	29 (3) 23-35	29 (1) 27-31	NS
P3	25 (3) 19-31	31 (1) 29-33	NS
P4	26 (3) 20-32	31 (1) 28-32	NS
P5	25 (2) 21-29	30 (1) 25-29	NS
P6	27 (2) 23-31	27 (1) 24-28	NS
P7	24 (2) 20-28	26 (1) 24-28	NS
P8	30 (3) 24-35	23 (1) 21-25	NS
P9	27 (2) 23-31	18 (1) 16-20	**
P10	33 (3) 27-39	17 (1) 15-19	**

Primary mass and primary total length can be assumed to be proportional to follicle size (Rohwer 1999), because feathers are generated by single rings or short cylinders of cells nested within each follicle. Assuming the diameter of feather calamus as an index of follicle size, both primary mass and total length can be related to calamus diameter by a linear regression. The variance explained by the model considering all ten primaries (Mass: $r^2 = 0.94$, $F_{1,8} = 129$, $p < 0.001$; Primary Length: $r^2 = 0.83$, $F_{1,8} = 38$, $p < 0.001$) increases of 4% and 15% respectively if P10 is excluded (Mass: $r^2 = 0.98$, $F_{1,7} = 434$, $p < 0.001$; Primary Length: $r^2 = 0.98$, $F_{1,7} = 307$, $p < 0.001$). For both regressions P10 lies outside the 95% confidence limits (Fig. 2).

The relationship between primary mass and total primary length was assumed to be a power curve. Power equations are most often used to describe size-correlated changes in shape (Redfern 1989, Worcester 1996). Also in this case, the variance explained by the model which considers all primaries ($r^2 = 0.993$, $F_8 =$

1141, $p < 0.001$, $b_0 = 4.0x10^{-5}$, $b_1 = 2.541$) increases if p10 is excluded, but only by 0.6% ($r^2 = 0.999$, $F_7 = 13723$, $p < 0.001$, $b_0 = 5.8x10^{-5}$, $b_1 = 2.461$). Again, P10 is outside the 95% confidence limits (Fig. 3).

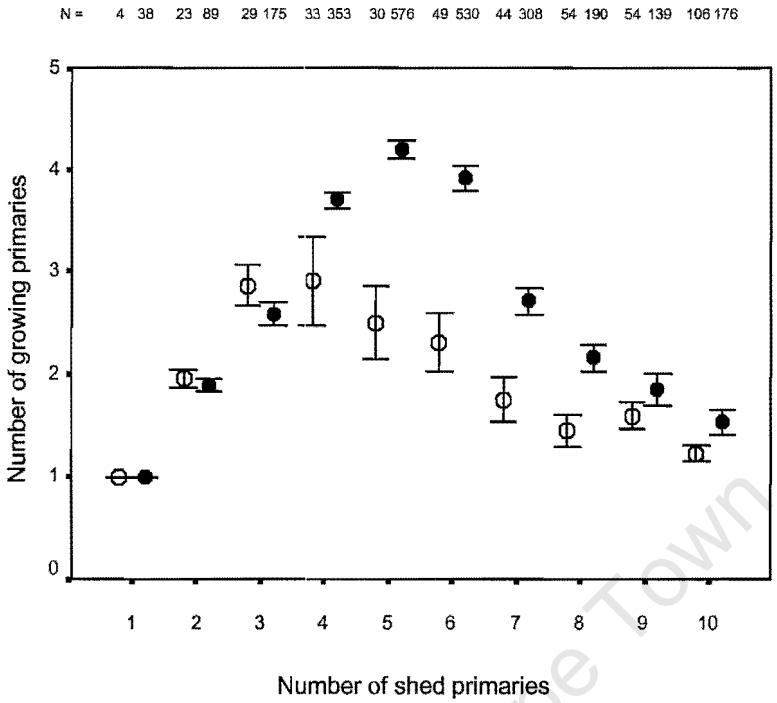

Fig. 1. Number of primaries simultaneously growing at various levels of primary moult in fast and slow moulting populations. Bars are 95% confidence limits.

Provided that environmental and bird physical conditions do not change, the relationship between primary growth rate (daily percentage feather-mass grown) and total primary length is expected to be linear or very close to linearity because both variables are proportional to follicle size. In slow moulting birds, this relationship can be assumed to be linear between P1 and P9 ($r^2 = 0.972$, $F_{1,7} = 239$, $p < 0.001$), with P10 as outlier (Fig. 4a). In fast moulting birds, on the contrary, the best fit of the point is given by a quadratic curve between P1 and P8 ($r^2 = 0.998$, $F_5 = 1133$, $p = 0.000$), with P9 and P10 as outlier (Fig. 4b).

The average total daily percentage feather mass grown, given for each bird by the sum of the daily percentage feather mass grown of each primary, increases linearly from P1 to P5 both in fast and in slow moulting populations (Fig. 5), although with different rates ($F_1 = 35.6$, $p = 0.000$). Slow moulting birds have a plateau between P6 and P10, while fast moulting birds show a pause in the increase only between P6 and P7, to be followed by a resumption of the rate of mass production from P8 to P10.

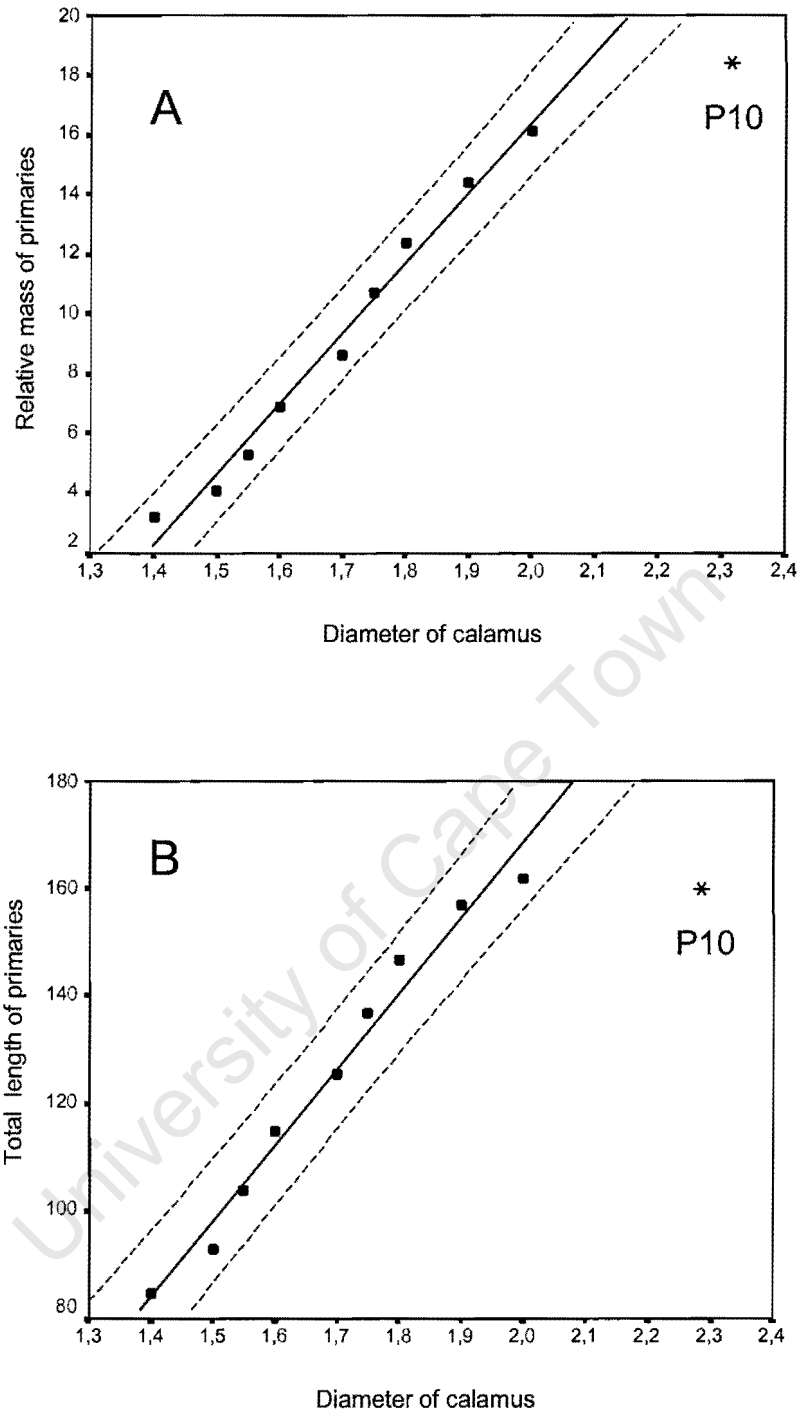

Fig. 2. Relative mass (a) and total length (mm) (b) of primaries in relation to the diameter of the calamus (mm). Solid line is the least-square regression fitted to the points (primaries from P1 to P9), dashed lines are 95% confidence limits. P10 is an outlier.

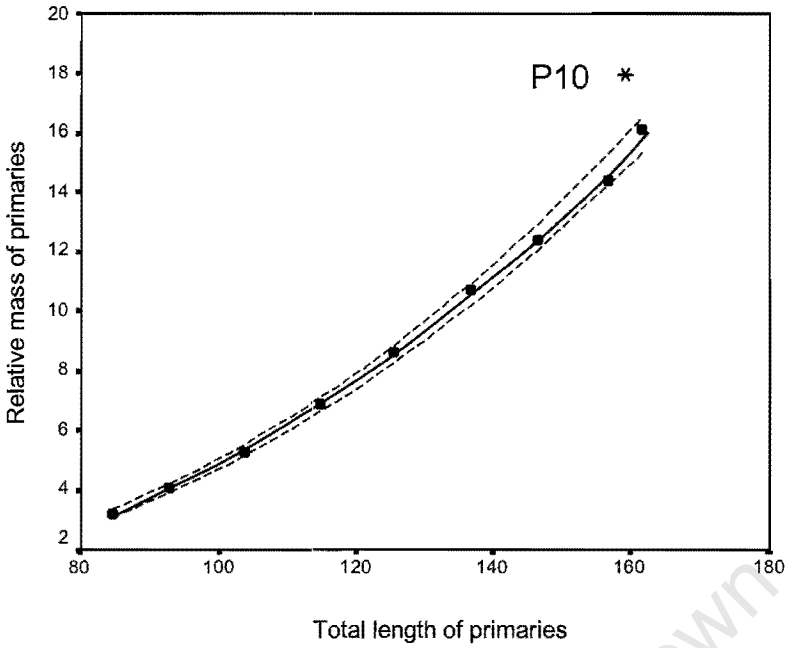

Fig. 3. The best fit of the relative mass of primaries from P1 to P9 on their total length (mm) is a power curve (solid line). Dashed lines are the 95% confidence limits. P10 is an outlier.

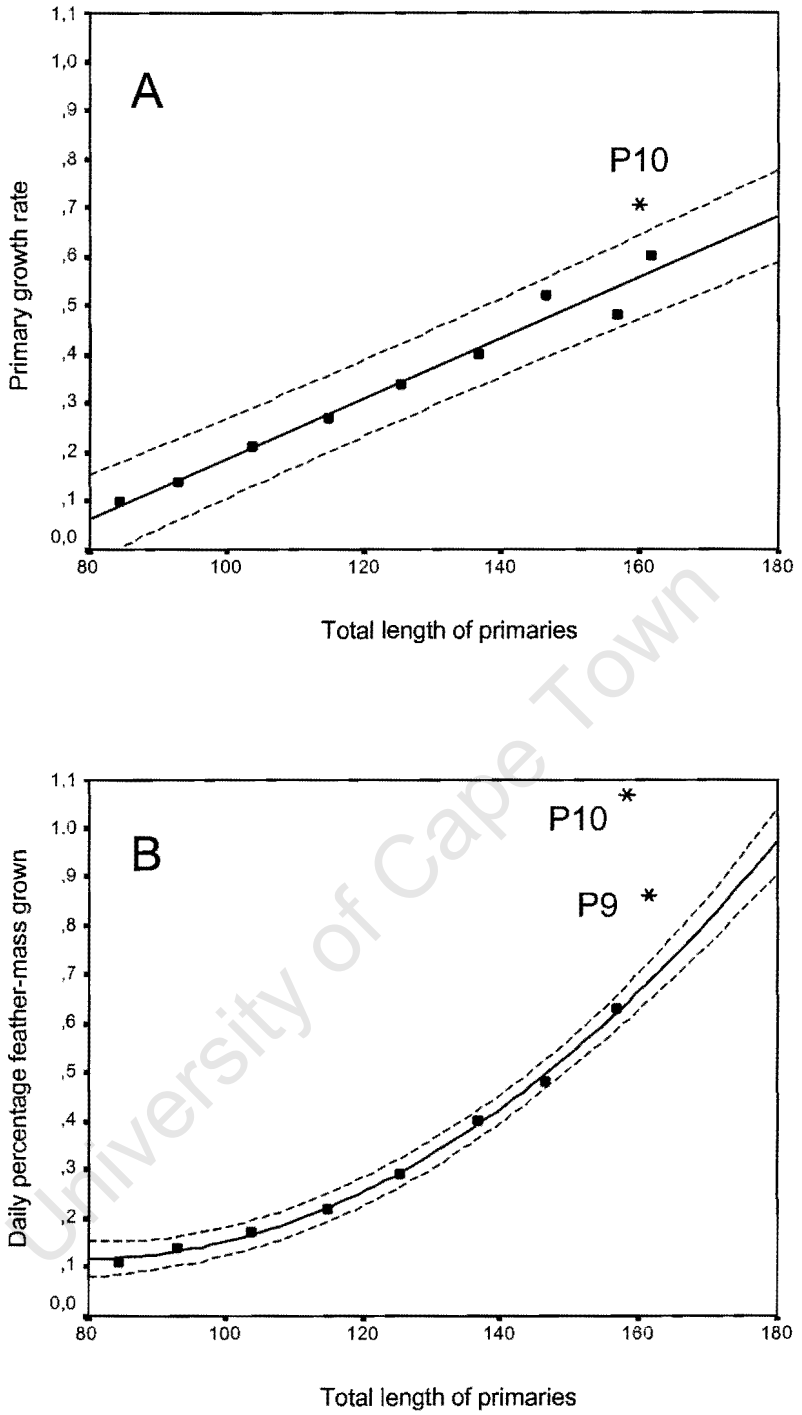

Fig. 4. Primary growth rates of slow (a) and fast (b) moulting populations on total length of primaries (mm). The relationship can be assumed to be linear in slow moulting birds (P10 outside the 95% C.L.), it follows a quadratic regression in fast moulting birds (P9 and P10 outside the 95% C.L.). Solid lines are regression lines, dashed lines are 95% confidence limits.

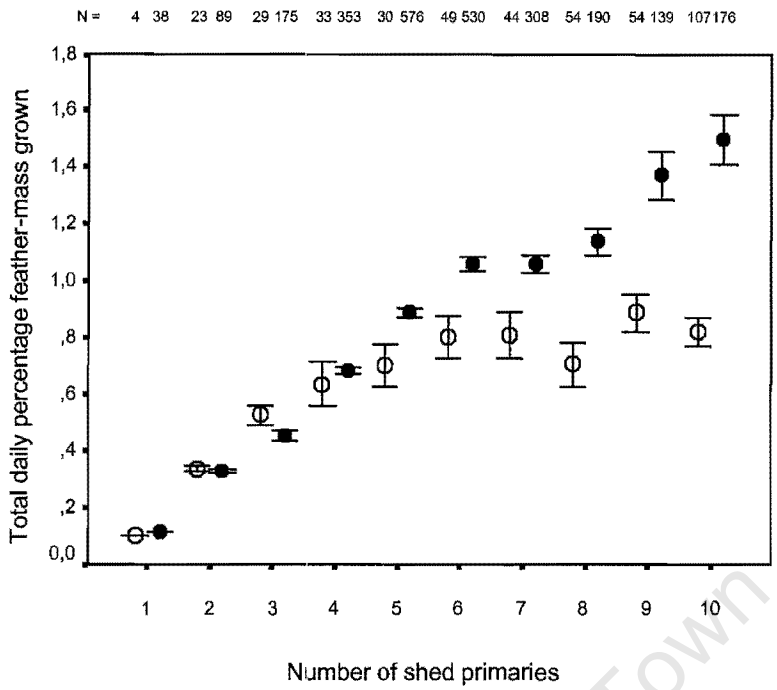

Fig. 5. Average total daily percentage feather-mass grown in relation to various moult levels. Mass grown was calculated considering for each bird all primaries simultaneously growing.

Discussion

Grey Plovers showed two distinct patterns of primary moult: a slow moult characteristic of populations wintering at sites with a mild weather and a fast moult characteristic of populations wintering at cold sites. Assuming latitude to be an index of winter conditions, no correlation with duration of moult was found, while mean starting date of primary moult was correlated to migration distance (Fig. 6a,b) (Serra 1998). This suggests that birds migrate at about the same speed along the various routes.

Primary moult speed can be regulated by varying the number of feathers growing at the same time and/or varying feather growth rates. Grey Plovers did both. The regulation of shedding rate is probably a widely used scheme at individual level. Among Charadriiformes, different shedding rates have been observed in Dunlins *Calidris alpina* (Hölmgren *et al.* 1993, Serra *et al.* 1998) and Black Terns *Chlidonias niger* (Zenatello *et al.* submitted).

It is generally accepted that feather growth rates are little affected by feather length or mass because these latter are both dependent on follicle size (Rohwer 1999). However, these data strongly suggest that, in Grey Plovers, this relationship holds true only for the feather tract P1-P9, while P10 differs from the other primaries, possibly because of a greater specific mass. This is confirmed by the relationship between feather mass and total length. An intuitive explanation for a heavier and hence possibly more resistant structure of P10 is that it forms the leading edge of the wing and must therefore accomplish different aerodynamic functions. It has been observed that the vanes of outer primaries are more resistant to out-of-plane forces than those of the inner primaries and the fact explained with the need to sustain larger aerodynamic forces in flight (Ennos *et al.* 1995).

The similar flexural stiffness observed among primaries with different relative positions (leading, central or trailing) on the wing (Worcester 1996) corroborates the hypothesis of structural differences (Redfern 1989)

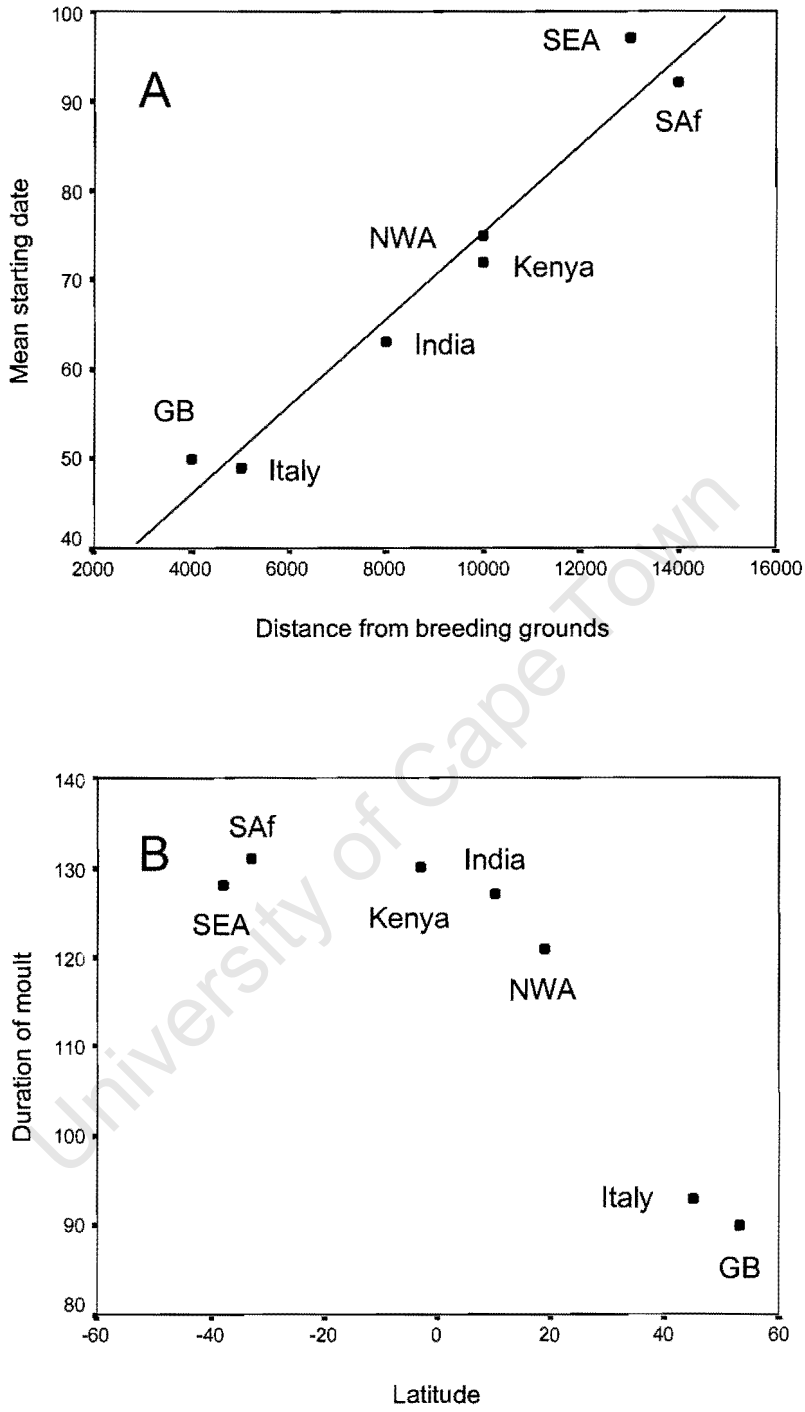

Fig. 6. Mean starting date on distance (km) from breeding grounds (a) and duration of primary moult (days) on latitude (b). Mean starting date is correlated with distance from breeding grounds ($r = 0.97$, $p < 0.001$) (from Serra 1998, moult parameters recalculated).

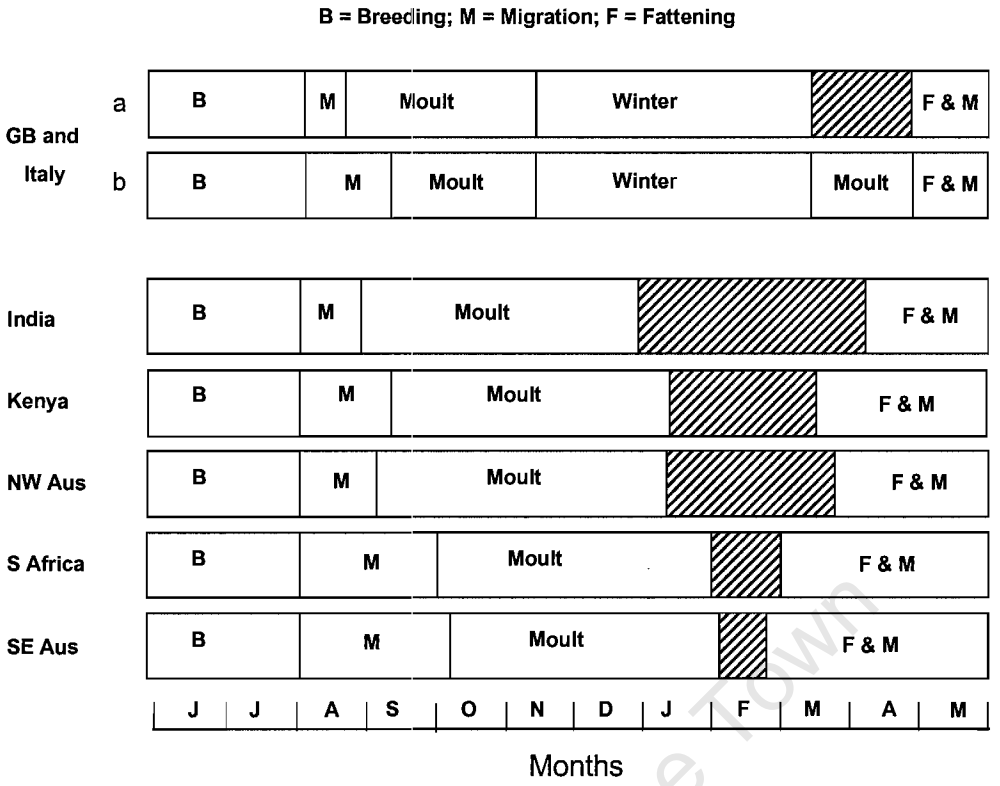

Fig. 7. Schedules of major phases in the annual cycle of seven Grey Plover populations (from June to May). The dashed areas are periods free from energetically costly events. In Great Britain and Italy, two patterns can be observed in relation to primary moult: (a) moult completed before the winter; (b) moult suspended before the winter and resumed in spring.

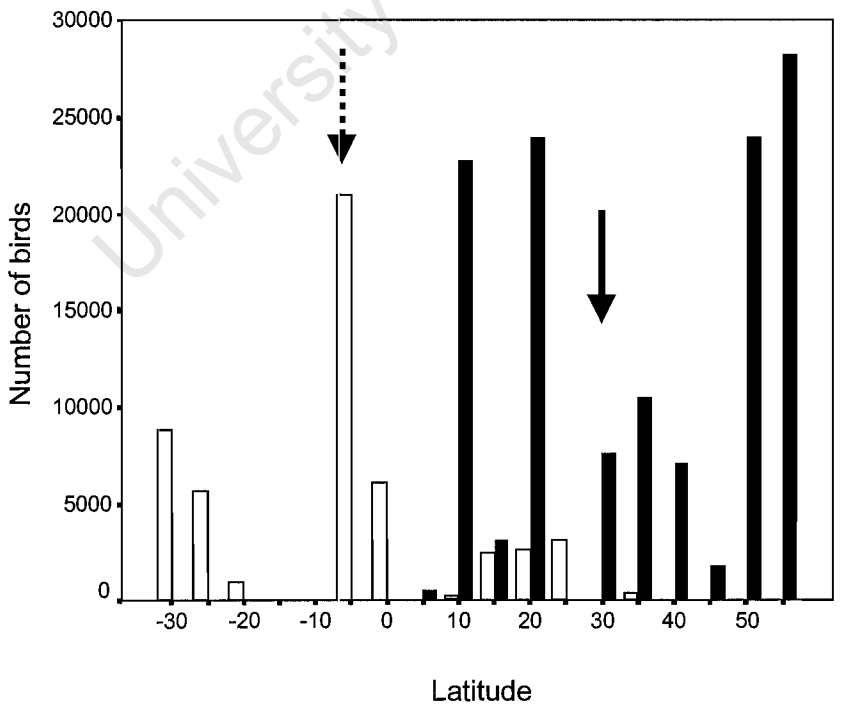

Fig. 8. Numbers of wintering Grey Plovers at different latitudes in the Afro-Palearctic system. Open bars are birds located along the West Asian-East African Flyway, filled bars are birds along the East Atlantic Flyway (see Appendix 1). Arrows indicate the median points of the distributions.

found that primary mass was proportional to length in a plot of nine primaries of five species. However, it is difficult to accept that primaries of different species can be effectively described by a single curve. We would rather suggest the existence of species-specific relationships, linked to wing shape and flight characteristics. A comparative study might shed some light on these aspects.

With the expected exception of P10, primary growth rates of slow moulting birds can be linearly correlated with primary length, suggesting that birds did not change primary growth rate during this period of moult. This might be an indirect confirmation that environmental and bird conditions at those sites were stable. In fast moulting birds, the quadratic relationship indicates that there was an acceleration of growth rates during the whole moult period, possibly linked to decreasing daylength and concomitant decreases in temperature, and that the function of increase changed at P9 and P10. This latter acceleration of feather mass production can be interpreted as a bird response to signals of winter arrival. An adaptive responsiveness of moult is supported by the fact that 35% of British Grey Plovers suspend primary moult just before winter when moult limit is at P9 or P10 (Branson & Minton 1976, Serra *et al.* in prep.). Hence, feather mass production is not constant throughout the whole moult period as it was previously hypothesised (Underhill & Zucchini 1988), but it can be regulated in relation to proximate needs, probably at an individual level. However, in slow moulting birds, mass production can be assumed to be constant between P6 and P10, i.e. when 72% of total primary mass is produced. This might explain why percentage feather-mass grown is rather effective in removing the curvature of moult score distributions (Summers *et al.* 1983). However, the assumption of linearity does appear to break down near the end of moult, and this topic needs further investigation in the application of the Underhill-Zucchini moult models.

The major events in the yearly cycle of the various populations are summarised in Fig. 7. Excluding the breeding period, assumed to be of equal length throughout their Palearctic breeding range, Grey Plovers have different 'time windows' available for moult and preparation for migration, determined by the length of the inter-migration period and by the presence of unfavourable environmental conditions. In northern populations, birds arriving late in autumn have insufficient time to complete moult and have to suspend it before the winter (Branson & Minton 1976, Serra 1998, Serra & Rusticali 1998, Serra *et al.* in prep.). At southern latitudes, moult suspension is virtually absent, and the moult period is shorter than the maximum time available (Balachandran *et al.* 2000, Minton & Serra 2001, Pearson & Serra 2002, Serra *et al.* 1999). Two points can be stressed: i) moult is constrained by time only in the northern populations and ii) moult speed does not fall below a given moult rate. Primary moult might not be spread throughout the whole inter-migration period because there is a trade-off between the risks of living a long period with an incomplete wing (i.e. higher predation risks, limited movement capacity in case of environmental crises or unpredictable conditions) and the need of growing high quality, long-lasting primaries to enhance survival outside the moulting period (Serra 2001). The period free from energetically costly events is longer at inter-tropical latitudes, and decreases moving both north- and southwards. In Britain and Italy, birds not completing the moult before the winter have no time free from major events. This might be a prime selective factor leading birds to accelerate primary feather growth before the winter.

Primary moult duration and feather quality might also contribute to explain why the barycentre of the Grey Plover winter distribution in the Afro-Palearctic migratory system, like that of many other Arctic waders, is around the inter-tropical zone (Fig. 8). This is the closest area to the breeding grounds where birds can find optimal moult conditions. Large numbers of wintering Grey Plovers in Europe are a recent acquisition on an evolutionary scale, having increased exponentially in the last thirty years (Moser 1988, Tubbs 1991, Cayford &

Waters 1996) and probably reflect a westward expansion of the breeding range. Data presented in this study suggest that primary moult patterns observed in Europe should be considered as individual adaptations to a new environment rather than the product of genetic evolution because they seem to be regulated by external factors. Investigating primary quality and primary growth rates of Arctic waders which have a long history of fast moults at northern latitudes, such as the Dunlin or the Purple Sandpiper *Calidris maritima*, might be rewarding because these species might have evolved different ways of producing high quality feathers in a short time.

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Appendix 1. Population estimates of Grey Plovers in their Afro-Palearctic wintering range. Countries with population estimates smaller than 100 birds were excluded.

	Location	Population estimate	Reference
East Atlantic Flyway	Dutch, German and Danish Wadden Sea	16 000	Meltofte *et al.* 1994
	Britain & Ireland	40 500	Tubbs 1991
	France (Atlantic)	24 000	Deceuninck & Maheo 2000
	France (Mediterranean)	250	Smit 1986
	Italy	2 000	Serra *et al.* 1997
	Spain	2 600	Dominguez *et al.* 1990
	Portugal	7 100	Dominguez *et al.* 1990
	Tunisia	20 500	Smit 1986
	Other Mediterranean countries	600	Smit 1986
	Morocco	15 000	Kersten & Smit 1984
	Canary Islands	300	Velasco & Alberto 1993
	Mauritania	24 000	Van Dijk *et al.* 1990
	Senegal	6 000	Schepers *et al.* 1998
	Gambia	350	Dodman *et al.* 1999
	Guinea Bissau	39 100	Salvig *et al.* 1994
	Guinea	23 400	Altemburg & van der Kamp 1991
	Sierra Leone	5 800	Tye & Tye 1987
	Liberia	300	Gatter 1997
	Ivory Coast	100	Thiollay 1985
	Ghana	1 700	Ntiamoa-Baidu & Grieve 1987
	Benin	100	Dodman & Taylor 1996
East African / West Asian Flyway	Caspian Sea	350	Summers at al. 1987
	Egypt	2000	Atta *et al.* 1994
	Saudi Arabia	7 000	Zwarts *et al.* 1990
	Oman	2 600	Green 1994
	Arabian Emirates	500	Smart *et al.* 1983
	Eritrea	2 500	Baccetti pers. comm.
	Djibouti	200	Ash 1985
	Gabon	7 200	Schepers & Marteyn 1993
	Kenya	5 000	Pearson & Serra 2002
	Tanzania	21 000	Bregenballe *et al.* 1989
	Mozambique	2400	Dodman *et al.* 1997
	Madagascar	200	Dodman & Taylor 1995
	Zimbabwe	100	Dodman *et al.* 1997
	Namibia	5 700	Summers *et al.* 1987, Underhill 1997
	South Africa	8 800	Summers *et al.* 1987, Underhill 1997